Trait similarity vs Species similarity in coral reef ecology:

Test of improved monitoring methods using Southwest Madagascar reefs

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Declaration

This thesis is submitted to the University of Warwick in support of my application for the degree of Doctor of Philosophy. It has been composed by myself and has not been submitted in any previous application for any degree.

The work presented (including data generated and data analysis) was carried out by the author except in the cases outlined below:

Ch 3: *The only data in this chapter collected by the author (jointly with Sophie Benbow, Blue Ventures) was clod card data for 3 reef sites, which was added to an existing clod card data set for 4 reef sites. Data presented on coastal bathymetry, large-scale currents, winds, cyclones, tides, sedimentation, and water temperature was compiled using reference texts, and satellite imagery data from NOAA and Blue Ventures.*

Summary

Trait-based approaches are emerging in various fields of ecology, and are here developed for coral reefs. 'Traits' means biological characteristics of each species; thus closely related species may have different traits and distantly related species may share common traits. This promotes understanding of a system better than using species alone.

Chapter One summarizes existing methods, mostly from plant ecology, explores their utility for corals, and an extensive review then extracts candidate *Scleractinian* traits (Chapter Two). A dataset of 26 key traits from 231 species from Southwest Madagascar was then collected using 68 reefs of several typologies along several natural and 'use' gradients (Chapter Three). This used over 7,000 photo-quadrats on reefs spanning over 200 km (Chapter Four).

Trait-based approaches require species-level identification. However, where species are difficult to distinguish, a species-replacement methodology facilitated translation of species to trait-combinations (Chapter Four).

Inter-specific trait similarity between the 231 corals and their 26 traits is examined (Chapter Five). In total, 13 groups of corals with highly similar trait-combinations were identified, in which species are functionally equivalent and which therefore can be considered as functionally interchangeable parts in the ecosystem. However, because one quarter of species had unique trait combinations, a functional group approach to surveying reefs may not adequately describe existing trait diversity. Therefore a methodological alternative to using functional groups alone was developed.

A trait-based similarity coefficient (*Tsim*) was developed to take into account both species and trait combination similarities between reefs (Chapter Six). A R-based package that calculates and visualizes *Tsim* is provided. *Tsim*'s characteristics were compared to species-based coefficients (Renkonen similarity). *Tsim* identifies functionally similar reefs missed using species identity alone (Chapters Six and Seven), and can be used to determine reefs that have highly similar trait combinations while being very dissimilar in terms of species.

Abbreviations

CPCe	Coral Point Count with Excel Extensions research software
Gsim	Gower similarity measure
Gdis	Gower disimilarity measure
GBR	Great Barrier Reef
Rsim	Renkonen similarity measure
Rdis	Renkonen dissimilarity measure
Tsim	Trait similarity measure
Tdis	Trait dissimilarity measure

1.
Introduction

" We can say something about the community by giving a list of its species composition, but a community is poorly described by such a list alone"

(Whittaker, 1975)

1.1. The renaissance of trait ecology

In order to communicate information about the natural world, human beings must often reduce the continuous aspects of natural organization into discrete units; this is the challenge of taxonomy. Since the time of Linnaeus the species has been the fundamental unit used to refer to, and communicate information about, living organisms. However, since Linnaeus the world population has increased more than a thousand-fold from around 600 million in 1700, to 7 billion in 2011. This exponential population growth has increased anthropogenic pressures on natural organization resulting in sharp decreases in species biodiversity. As a result scientific focus has shifted from classification of taxon to understanding how decreases in species diversity impacts overall ecosystem functioning (Ehrlich and Wilson, 1991, Chapin III et al., 2000).

Investigations into how species diversity relates to ecosystem functioning have been largely unsuccessful and have failed to produce general principles (Lawton, 1999, Simberloff, 2004, McGill et al., 2006). From the early 1960s, community ecology has focused largely on pair-wise species interactions (Whittaker, 1975, Ricklefs and Travis, 1980, Lawton, 1991), which were later scaled up into community models. These had some success in representing systems with a few species, but largely struggled to produce general principles about more realistic multi-species systems (Lawton, 1991, Simberloff, 2004). Despite these shortcomings, the most recent US National Science Foundation panel's recommendations for population and community ecology continues to push the research agenda for species level approaches (Agrawal et al., 2007).

To address the shortcoming of species-only approaches a renaissance of sorts is taking place in community ecology (McGill et al., 2006): species-level data is being supplemented with trait-level data in some systems. It has been discovered that functional trait diversity plays an important role in: ecosystem processes (Hooper et al., 2005), the resilience of ecosystems to environmental stressors (Folke et al., 2004), and the provision of ecosystem services (Díaz et al., 2007). While trait-based approaches have shown great promise in other branches of ecology, such as plant ecology (Shipley et al., 2006) it remains largely unexplored in marine and especially coral reef ecology.

Marine ecology has a strong tradition of focusing on the species level (Connell, 1961, Paine, 1966, Paine, 1969). There is however much to be gained from quantifying the abundance and diversity of traits alongside species as this allows one to link empirical measurements on the species level (i.e. *Symbiodinium* association versatility) directly to macro-scale functioning (i.e. resistance and resilience to bleaching).

Another reason for embracing trait-based approaches in coral reef ecology is that in *Scleractinian* corals the species concept is in a state of flux. Veron (2011) suggests that the only natural unit with which one can describe *Scleractinian* corals is the syngameon, a unit reproductively isolated in time and geographic space which can consist of one or many genetically linked species . Where a syngameon contains multiple species, it may be distinct at a particular geographic location, but because it can reproduce with other species in other locations (and thereby generate hybrid species) it becomes immersed in a patchwork of morphological variation. Ultimately taxonomic decisions determine the morphological variation and geographic range of a particular 'species, and 'species' taxonomic boundaries can dissect natural continua. To delineate a syngameon is difficult and impractical for use in taxonomy (Veron, 2011).

Coral species-level trait information is becoming more abundant. The most recent European International Society for Reef Studies (ISRS) Symposium in 2010 presented a wealth of new data on coral and coral larvae physiology including: coral growth rates, species-specific stress responses to thermal, photo, and elevated pCO_2,

and *Symbiodium* clade versatility just to name a few. Compiling this trait-level information for each coral species, standardizing, and citing entries in a freely accessible online database would greatly facilitate undertaking trait-level studies in reef ecology.

As well as specific species trait studies, theoretical discussions have been accumulating on how coral species biodiversity influences larger ecosystem properties (i.e. ecological phase-shifting, resilience, stability etc.). As Loreau (2010) describes in a recent review, one of the main obstacles between unifying community ecology and ecosystems ecology has been 'the gap between the macroscopic, holistic perspective approach of macro ecology and the more microscopic, mechanistic perspective of community ecology.' This gap is clearly evident in reef ecology as ecosystem functioning and stability theories have yet to be linked to smaller scale, mechanistic variables such as life history traits. The intent of this review is to provide a starting point for reef ecologists interested in bridging our understanding of the relationships between reef-level and species-level properties using coral life history traits.

Here I firstly review the benefits of incorporating trait-based approaches into coral reef ecology. I briefly review four main methodological areas of trait-based ecology: 1. trait indices, 2. functional classification, 3. modelling species interactions, and 4. linking traits to environment reviewing any coral studies in these four methodological area to date.

1.2. Advantages of using trait-based ecology

1.2.1. Traits link species diversity to ecosystem properties

Biodiversity on the planet is decreasing at an alarming rate and many have compared the current extinction with mass extinction events that have occurred in past geological eras (Diamond, 1989, Smith, 1993, Morris and Heidinga, 1997, McKinney and Lockwood, 1999). Half of the world's extant species might become extinct under current patterns of global change (Smith, 1993). Not surprisingly, there

is great concern over how this enormous decrease in diversity will affect ecosystem functioning and provision of ecosystem services.

While the relationship between species diversity and ecosystem properties is complex, using traits rather than species may help clarify relationships and reveal general principals. This has yielded interesting properties and discussions for several ecosystems other than reefs, (McGill et al., 2006, Shipley et al., 2006, Whitham et al., 2006, Cingolani et al., 2007, Mcgill et al., 2007, Savage et al., 2007, Violle et al., 2007, Bremner, 2008, Weigelt et al., 2008, Cornwell and Ackerly, 2010, Vellend, 2010, Shipley et al., 2011); reef studies therefore can be informed by several areas.

1.2.1.1. Species diversity, ecosystem stability, and insurance

A number of experiments which have manipulated species diversity have found that increased diversity resulted in stabilization of ecosystem properties in both grassland plant communities (Tilman et al., 2006) and aquatic food webs (Steiner et al., 2005). However, the relationship between population-level stability and species diversity has been shown to range from positive (Romanuk and Kolasa, 2004, Steiner et al., 2005) to negative (Gonzales and Descamps-Julien, 2004, Tilman et al., 2006). This relationship variability suggests that the diversity-stability theory is missing key elements.

Two closely related hypotheses, the 'portfolio effect' (Doak et al., 1998, Tilman, 1999) and the 'insurance hypothesis' (Yachi and Loreau, 1999) predict that due to the asynchrony of species responses to environmental fluctuations, ecosystem properties will be less variable in a system with high species diversity than one with low species diversity. While this may sometimes be true, one species can only 'replace' another if it has the same combination of traits (component functionality). Species diversity, in other words, may not equate to an ecosystem with high functional redundancy.

Despite theoretical uncertainty, species biodiversity as insurance of continued ecosystem services provision has been formally incorporated into ecological

economics (Armsworth and Roughgarden, 2003, Baumgärtner, 2007). While it is important to place an economic value on species diversity for the sake of conservation, it is equally important to supplement species diversity data with trait diversity data and improve understanding of how the two relate to ecosystem resilience.

Examples of how high diversity coral systems can fail to recover after environmental impacts were highlighted during the 1998-bleaching event, the largest coral bleaching event on record. Some reefs located in the coral triangle, a region in the central indo-pacific hosting the greatest coral species diversity in the world, did not recover from the bleaching events, while reefs located in regions with lower levels of coral species diversity were able to recover from the bleaching event (see for example Wilkinson, 2008).

1.2.1.2. Species diversity and ecosystem process magnitude

Whilst the idea that greater plant diversity results in greater biomass production dates back to Darwin (McNaughton, 1993), positive short-term effects of species biodiversity on the magnitude of ecosystem processes (biomass, carbonate production etc.) has only relatively recently been confirmed through large scale experiments (Naeem et al., 1994, Naeem et al., 1995, Tilman, 1996, Hooper and Vitousek, 1997, Tilman et al., 1997, Hector et al., 1999). Loreau (2000) identified two central mechanisms by which species biodiversity influences ecosystem process. The 'complementarity effect' is where trait variations between species facilitate permanent association between species, which then enhances collective ecosystem performance. Secondly the 'selection effect' promotes dominance by species that exhibit extreme trait values. Therefore in understanding better how coral species diversity influences the magnitude of ecosystem process it is critical to use trait data to bridge species and ecosystem process data.

1.2.1.3. Diversity and ecological 'phase-shifts'

Worldwide, coral reefs have been observed to undergo dramatic changes in composition from coral dominated systems to systems dominated by algae (reviewed by Done, 1992, McCook, 1999, Nyström et al., 2000, Szmant, 2002, McManus and Polsenberg, 2004) or other non-coral assemblages (reviewed by Norström et al., 2008). These dramatic 'phase shifts' are still poorly understood. However, models of coral reefs as dynamic systems with non-linear behaviour suggest that critical tipping points and alternative stable states may exist (eg. Knowlton, 1992, Mumby et al., 2007, Norström et al., 2008, Nyström et al., 2008, Fung et al., 2011).

One reason for the lack of progress in phase-shift research is the scale over which changes in community composition are measured. At one common extreme, all *Scleractinian* corals may be amalgamated into one category, 'hard coral cover'. While simplifying field work, this obscures ecologically important shifts in coral community composition (Hughes et al., 2010). Coral species exhibit differential mortality and replenishment capabilities and therefore two reefs with a similar percentage of hard coral coverage may respond very differently when faced with the same stressor. As a result, the coral composition of reefs worldwide is changing as a result of differential mortality and replenishment (Hughes and Connell, 1999, Hughes et al., 2003, Baker et al., 2008, Adjeroud et al., 2009). A functional group approach to understanding reef phase-shifts has been suggested to help with the need for grouping species while retaining simplicity in the field (Nyström et al., 2008).

In addition I suggest using trait diversity indices (discussed later) to understand how shifts that occur within coral populations relate to reef resilience. Modelling reefs in terms of coral trait availability could give insight into aspects of phase-shifts such as: dynamics of thresholds, reinforcing feedbacks, hysteresis and the reversibility of phase-shifts. Understanding underlying dynamics associated with phase-shifts is of great importance to developing functional and trait-based management on reefs (Bellwood et al., 2004).

1.2.2. Predicting species assemblages under environmental scenarios using traits

If we disregards intraspecific trait variation, the traits possessed by a species can be likened to the playing cards it can use in a game where the rules are set by the prevailing environmental conditions. For any particular set of environmental conditions either one or several optimum trait sets (winning hands) exist for exploiting the available resources. Species compositions under particular environmental conditions can therefore be predicted using the trait combinations that they possess. For example, Shipley et al. (2006) were able to predict 94 percent of the variance in the relative abundance of plant communities along a 42-year sequence of secondary succession in twelve abandoned vineyards in Southern France using eight plant traits and entropy maximization techniques borrowed from physics. They suggested that the regular change in traits observed is due to a process they termed 'environmental filtering'; that is, for any environmental scenario (in their case field age), 'optimal' sets of traits values exist; the closer a species' set of traits is to an optimal trait set the more successful (abundant) that species will be.

In addition to predicting species abundances, maximum entropy techniques have also been used to predict the shape of species abundance distributions (Salvador et al., 2007) geographic distributions (Phillips and Dudik, 2008), and links in food webs (Williams, 2010). These techniques, while relatively new (Petchey, 2010), may prove to be very useful predictive methodologies in coral reef ecology.

1.2.3. Using trait-based indices allows for better placement of MPAs

Given the limited resources of both governmental and non-governmental conservation organizations, it is often not possible to protect all reefs equally and decision often have to be made regarding which reefs to designate and enforce as Marine Protected Areas (MPAs). Quantifying the coral trait composition of candidate MPA reefs and relating reef trait composition to the ability of each reef to resist and recover from local stressors would aid in highlighting potential reefs for designation as MPAs. By supplementing common species diversity indices with trait indices, reef managers would be better informed regarding which reefs would likely do well as MPAs. This is proposed later.

1.3. Trait terminology and framework

Since Darwin's famous work (1859), traits were considered mostly as proxies of organismal performance. However, developments mainly in plant community ecology (Grime, 1974, Petchey and Gaston, 2002, Shipley et al., 2006, Laliberté and Legendre, 2010, Pavoine et al., 2010) and plant ecosystem ecology (Chapin III, 1993, Grime, 1998, Lavorel and Garnier, 2002, Eviner and Chapin III, 2003) have broadened the use of the trait concept to studies that range from the gene to ecosystem level. The diversity of trait types and scales of application used in different disciplines resulted in a range of definitions and usages, leading to some confusion, although a number of recent reviews have reduced the ambiguity in terrestrial systems (Semenova and van der Maarel, 2000, Blaum et al., 2011) and have provided frameworks for trait organization (Lavorel et al., 1997, Whitham et al., 2006, Savage et al., 2007, Violle et al., 2007, Suding et al., 2008, Gross et al., 2009, Webb et al., 2010).

1.3.1. Traits and attributes

Here I follow the terminology and trait frame work of Violle et al. (2007) and define a trait as 'any morphological, physiological, or phenological features measured at the individual level'. As corals are animals not plants, I add to this trait definition behavioural features (mainly aggression, feeding, and sediment rejection behaviours). As corals are colonial animals I consider the individual to be both the polyp and the colony. Therefore traits measurable at the polyp level (tentacle length, calice width etc.) and colony level (colony morphology, surface to volume ratio etc.) are both included. The value of a trait at a particular place and time is referred to as an 'attribute' (Lavorel et al., 1997). Attributes can be either continuous (i.e. linear extension rate which is measured in cm yr^{-1}) or categorical (i.e. a coral's sexual system can be either spawning, brooding, or both).

1.3.2. Trait variability

Attributes can vary between different coral species (inter-specific variability) and between individual of the same species under the same environmental conditions

(intra-specific trait variation). These two types of trait variation are summarized in Figure 1.1.

Ideally coral trait databases should contain the mean and variance of the trait as well as the environmental conditions under which the measurements were made, as has been done for recent plant databases (Knevel et al., 2005, Garnier et al., 2007), for a temperate sponge (Bell et al., 2002), and cup coral (Bell and Turner, 2000). This is an important step in building a trait library that includes both the intra-specific variability and variability along environmental gradients.

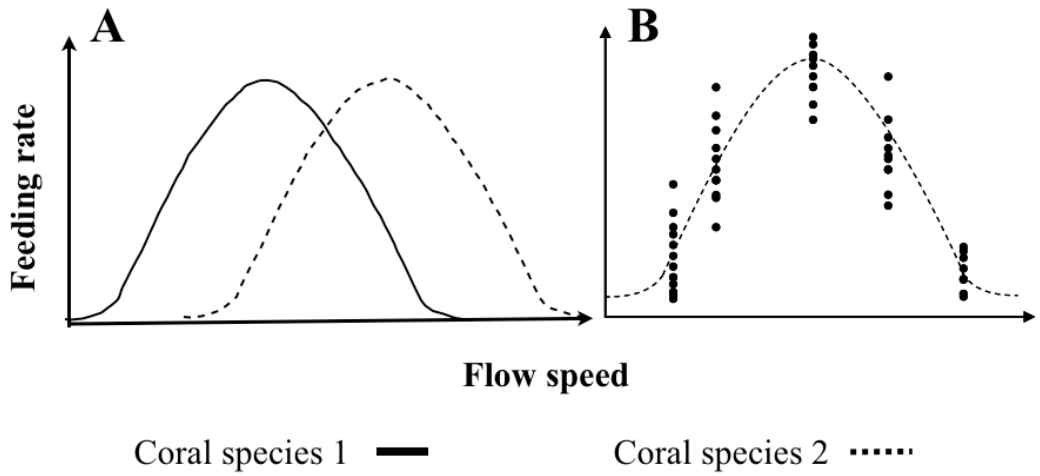


Figure 1.1 Theoretical example of trait variability along an environmental gradient A.) between corals (inter-specific variability) and B.) between individuals of the same species under the same environmental conditions (intra-specific variability).

1.4. Traits-based methods for reef ecology

Four methodological approaches central to trait-based ecology are: 1.) measuring aspects of trait diversity using indices, 2.) using traits to groups species into functional groups and guilds, 3.) modelling species interactions using traits and 4.) linking patterns of trait distribution with environmental variables. For each methodological area I review the available trait-based coral studies conducted to date.

1.4.1. Coral trait diversity metrics

Trait diversity, also commonly referred to as functional diversity, is the diversity of functional traits possessed by a set of coexisting species. While functional diversity does not take into account any phylogenetic relatedness, species diversity and functional diversity indices may be closely related since 1.) closely related species often have similar phenotypic traits and 2.) numerical methods for calculating functional diversity and species diversity are similar.

Functional diversity can be divided into functional richness, functional evenness, and functional divergence (Mason et al., 2005). When taken together, these three complementary facets describe both the distribution and abundance of species in trait space (a multi-dimensional space where each axis represents a trait). Knowing the distribution and abundance of a community's species in trait space can then give insights into the functional redundancy present within the ecosystem and may highlight any particular areas of vulnerability to stress. For example, if the coral trait space representing high thermal tolerance is empty, one can infer that the reef is sensitive to bleaching events.

1.4.1.1. Functional richness -the occupation of trait space by species

Species can be ordinated in trait-space. The total volume that species occupy in trait space, as delimited by the most extreme species, is known as the functional richness or FRic (Villéger et al., 2008) or convex hull volume (CHV; Cornwell et al., 2006). The CHV takes into account only presence or absence of species and traits without considering their abundance (see Figure 1.2). CHV is sensitive to trait units, however Cornwell et al. (2006) has identified rescaling procedures that have proved highly reliable for use with communities exhibiting large CHV values. Importantly, CHV can only be used for scenarios where there are more traits than species. Analysis for N traits requires at least N+1 species; otherwise the volume would be 0 (since two points are needed to define a distance, 3 to define an area, four to define a three-dimensional volume and so forth).

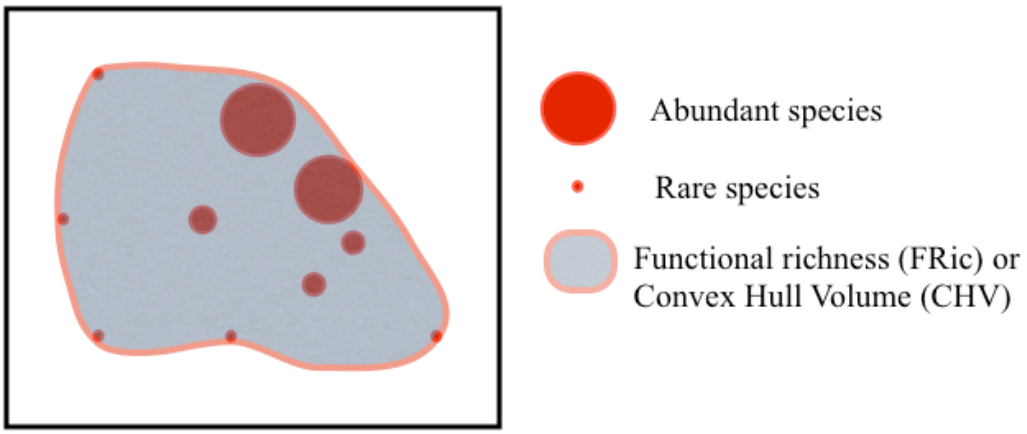


Figure 1.2 Compressed 2D representation of functional richness (FRic; indicated by grey shading), which is total volume that species occupy in trait space, as delimited by the most extreme species. Note that FRic is independent of species abundance.

1.4.1.2. Functional evenness –regularity of species abundance in trait space

Functional evenness, quantified using FEve (Villéger et al., 2008), refers to how regularly species are distributed in trait space, weighted by their abundance. It takes into account both evenness of the spacing of species in trait space and the evenness of their relative abundance. If all species are equidistance from one another in trait space and have the same abundance, then the index is one. The index decreases towards zero as the abundance and species distance becomes more uneven (see Figure 1.3). FEve can be used without species abundance if one is only interested in examining the spacing of species in trait space (see simplification in Weiher, 2011). To calculate FEve a community must contain at least 3 species.

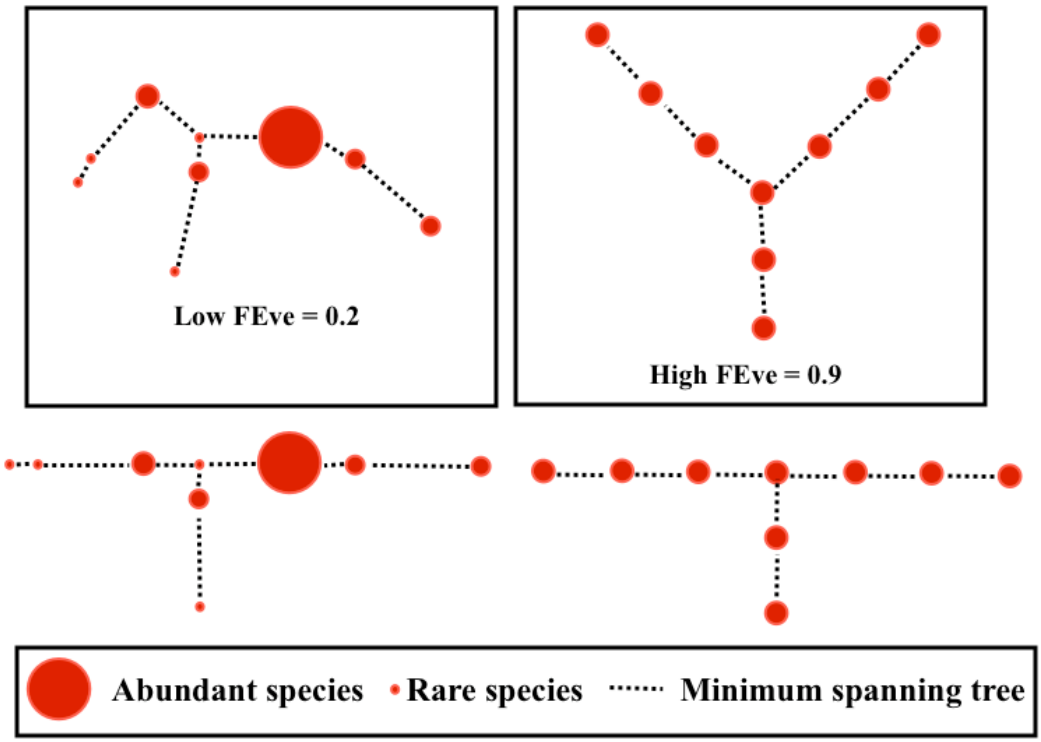


Figure 1.3 The top diagrams show a compressed 2D representation of functional eveness (FEve), which refers to how regularly species are distributed in trait space, weighted by their abundance. FEve takes into account both the evenness of the spacing of species in trait space and the evenness of their relative abundance. In the bottom diagrams the minimum spanning tree between the species has been flattened to emphaisze how species abundance influences FEve.

A disadvantage of FEve is its independence of the convex hull volume or total trait space. This means that while FEve can give an indication of the evenness of the weighted distribution of species relative to each other it does not provide information on the eveness of the species distribution within the entire trait space.

1.4.1.3. Functional divergence –distance of species from the centroid of trait space

Functional divergence of FDiv (Villéger et al., 2008) is the abundance-weighted distance of species from the centroid of trait space (see Figure 1.4). When abundant species also have the most extreme trait values FDiv is high and when they have trait values closer to the trait space centroid FDiv is low. When communities are exposed to extreme environmental conditions (filters), species with traits specialized for such conditions are likely to persist. Species with traits specialized for survival in extreme

environmental conditions are unlikely to be highly abundant under more 'normal' conditions since they would be outcompeted by species more adapted to such conditions. Therefore a high FDiv value could be an indication of a community that has shifted its trait composition in response to extreme environmental conditions that could be natural (i.e. the high flow conditions found on the reef crest) or anthropogenic (i.e. warming events) in origin.

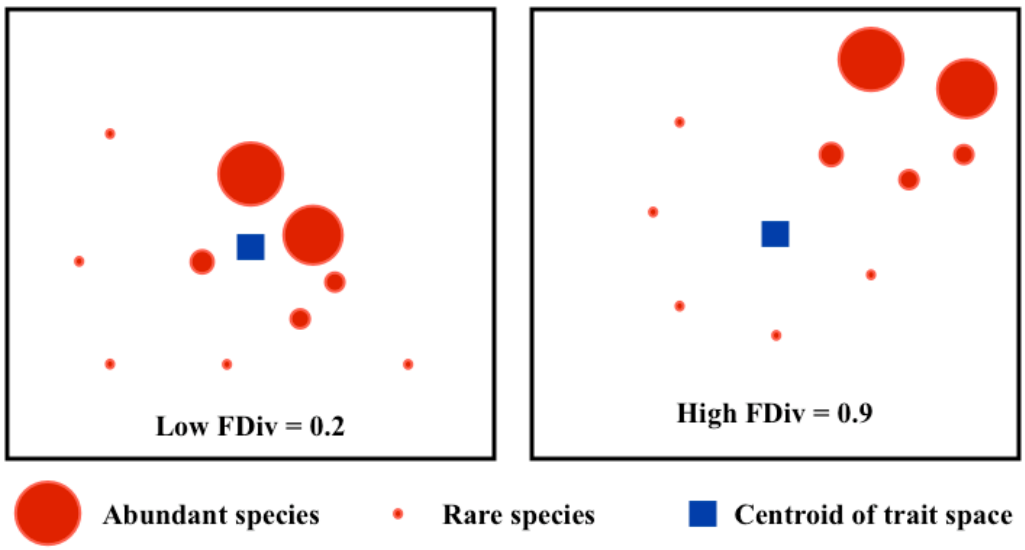


Figure 1.4 Compressed 2D representation of functional divergence (FDiv), which is the abundance-weighted distance of species from the centroid of trait space (blue square). When abundant species (large red points) are the furthest from the centroid (i.e. have uncommon traits), FDiv is high (right diagram). On the other hand, if abundant species are nearest the centroid (i.e. have common traits) then FDiv is low (left diagram).

1.4.1.4. Other functional diversity indices

The occupation of trait-space by species can also be measured by several other indices (Petchey and Gaston, 2006, Lavorel et al., 2008, Mouchet et al., 2010, Weiher, 2011).

Somerfield et al. (2008) recently introduced a measure of 'average functional distinctness' or x^+ and demonstrated its application using the traits for 70 English groundfish species. The average functional distinctness of a community measures the average similarities for all pair-wise comparisons between all the species present in a

community in terms of the traits they possess. Average functional distinctness is a percentage. Like other relatedness measures, x^+ can be displayed through ordination methods such as multidimensional scaling (MDS).

This ordination method is useful for the initial visual exploration of data. However, as it does not incorporate species and trait abundance it is sensible to supplement this method with other trait metrics that include abundance (i.e. FDiv).

1.4.1.5. Use of functional diversity metrics in reef ecology to date

To my knowledge, these functional diversity indices have not yet been applied to coral reef ecology. Incorporating trait indices into reef studies is becoming easier as tools for calculating FRic, FEve, and FDiv have recently been made available through the development of an R-based FD package (Laliberté and Legendre, 2010).

1.4.2. Guilds and functional grouping of corals

1.4.2.1. Background

Hutchinson (1959) poses the question "why are there so many different kinds of species?" He then goes on to develop the theory that competition for limited resources is responsible for delineating niches. This ground-breaking theory paved the way for work on grouping species in communities based on resource utilization. Within this framework Root (1967) coined the term "guild" and Cummins (1974) the parallel term "functional group." The term 'guild' refers to groups of species with similarity in resource sharing and is described more in terms of structural criteria (i.e. morphological structures such as beak shape allow birds to exploit different prey resources). In contrast, the term 'functional group' refers to groups of species that process resources and/or habitat features in the same manner and therefore impact on the same ecosystem process. In many ways guilds and functional groups are two sides of the same coin since species within a 'guild' that compete for the same resource will often (but not always) impact on the same ecosystem processes (Precht, 1994, Blondel, 2003).

1.4.2.2. Functional classification and their use in coral reef ecology

In coral reef contexts, extensive searching revealed only five functional classification schemes. Here I discuss Lavorel's four functional classification schemes and present the five reef studies within Lavorel's framework. I then discuss why equating colony morphology with functional groups without clearly stating objectives is inappropriate.

The grouping of species based on their traits should always be done with a specific objective. For example, if we are concerned with modelling reef rugosity then we should base our functional groups on traits associated with three-dimensional structure. On the other hand if we were concerned with modelling reef accretion rates we would consider coral traits such as density and growth rate. Therefore grouping is only suitable within the framework of the ecological functions being considered. In order of increasing specificity of objective Lavorel's (1997) groups for plants are: emergent groups, strategy groups, functional types, and specific response groups.

1.4.2.3. Emergent groups

Emergent groups are groups of species with biological attributes that naturally correlate with one another. Emergent groups 'emerge' as clusters of species in trait space due to tight correlations between traits. Often, but not always, such clusters of species with similar sets of attributes have evolved to exploit a particular resource and can therefore be considered a guild. If this guild then also has similar influences on ecosystem processes it is also a functional group.

I could not find any studies that searched for emergent coral groups using multiple traits. However, a number of studies have done simple correlations between two coral traits (see for example Porter, 1976).

1.4.2.4. Strategy groups

Species within the same strategy group have similar attributes as a result of similar patterns of resource use; they can therefore also be called guilds. Only one study has examined reef dynamics explicitly in terms of strategy groups. Murdoch (2007),

adapted Grime's famous 'Competitor-Stress tolerant-Ruderal (C-S-R) Triangle Theory' on plant strategies to predict coral composition for reefs in both Florida and Bermuda. Murdoch divided coral species into five groups: branching-oviparous, branching-viviparous, massive-oviparous, massive-viviparous, and plating/solitary-viviparous based on 10 life-history traits (see Table 1.1.). Murdoch then identified each group as belonging to one or two of Grimes 'competitor', 'stress tolerant', and 'ruderal' groups.

Table 1.1 Murdoch's five coral strategy groups for Caribbean corals and their ranking in 10 critical traits. The groups are named by colony morphology (blue) and reproductive category (red). Smaller number represent higher rank and greaterlevels of each attribute. The adaptive strategy which most closely represents the strategy group are given (C: Competivite; CR: Competitive ruderal; CS: Competitive-Stress tolerant; R: Ruderal; S: Stress-tolerant). These adaptive strategies are based on Grime's C-S-R Triangle theory for plant strategies. Table adapted from Murdoch (2007).

Trait	**Branched oviparous**	**Branching viviparous**	**Massive oviparous**	**Massive viviparous**	**Plating or Solitary Viviparous**	**Reference**
Maximum size (genet)	1	3	2	5	4	Johnson et al. 1995
Longevity (ramet)	3	4	2	5	1	Hughes 1984
Longevity (genet)	1	2	3	5	4	Highsmith 1987
Reproductive maturity	5	2	4	1	3	Richmond 1998
Reproductive effort	4	2	3	1	5	Richmond 1998
Reproductive method	F>X	F:X	F>X	F<X	F<X	Highsmith 1987
Growth rate	1	2	3	4	5	Huston 1985
Stress response	3	4	2	5	1	Bak and Meester 1998
Aggression	3	4	5	2	1	Lang 1973
Palatability	3	2	4	1	5	Rotjan and Lewis
Adaptive strategy	C	CR	CS	R	S	Murdoch 2007

1.4.2.5. Functional types

Functional types are groups of species that have similar functional roles in ecosystem processes due to similar responses to multiple environmental factors. Since functional types focus on ecosystem processes they are classified as functional groups rather than guilds. Functional types in coral reef ecology have been

recognized as far back as Walther (1888; according to Ginsburg and Schroeder (1973, p. 605); not seen by EW). Walther recognized corals as being separated into three main functional types: 'frame-building', 'frame-binding' and 'sediment-producing and trapping.' Klement (1967), recognizing the importance that an erect morphology had on slowing down or baffling currents allowing sedimentation to drop from the water column, added a fourth functional type: 'bafflers.'

Fagerstrom (1991) presented a hierarchy of rather subjective criteria for partitioning corals into 'Constructor', 'Baffler' and 'Binder' functional types similar to those presented by Walther and Klement (see Table 2). Although Fagerstom presents his three groups as guilds, they are not guilds, as the groups are not competing for a common resource. The misuse of the term guild by Fagerstrom and others in reef ecology has been reviewed by Precht (1994). Rather than sharing a common resource, the constructor, baffler, binder groups are describing reef accretion, which is important to the sedimentologists and geologists that most frequently use these groupings to describe modern and ancient reefs.

Table 1.2 Fagerstroms checklist for assigning corals from both modern and ancient reef to one of three functional types based on how they contribute to reef construction adapter from Fagerstrom, 1991). The traits biostratonomy and skeletal packing density were not included as they are mainly of interest to palaeontologist.

Criteria	Constructor	Baffler	Binder
Dominant growth direction	Upwards	Upwards	Lateral
Colony morphology	Massive, domes, branches, cups, columns	Cylinders, cones, blades	Sheets, lenses, runners, webs, plates, umbrellas
Skeletonization	Well skeletonization, stron, rigid	Poorly skeletonized, mostly as skeletal fragments	Well-skeletonized
Colony size	Large	Small	Medium
Colonality	Colonial	Solitary or colonial	Colonial

1.4.2.6. Specific response groups

Specific or functional response groups are groups of species that exhibit similar responses to specific environmental factors (i.e. bleaching resistant corals). A specific response group is not a functional group in the strictest sense because its member species do not process resources similarly nor do they necessarily impact the same on ecosystem processes. Rather specific response groups can be thought of as groups of species that pass through environmental filtering events (i.e. storms, warming events, disease outbreaks) with similar success rates. I identified three studies in the coral literature that used specific response groups based on coral traits.

Disease can be considered a filtering event through which groups of corals can pass with varying degrees of success. Diaz and Madin (2011) identified a specific response group to disease (although they did not identify it as such) which they simply termed corals with 'disease potential'. A coral was observed to have 'disease potential' if it had been observed in the literature in a diseased state. Diaz and Madin used a general linearized model to examine the influence of 9 coral 'traits' on membership in the disease potential groups. They found most of the traits had some influence on membership to the 'disease potential group' when examined alone, however, when analysed together predator diversity, geographical range size, and characteristic local abundances were the main predictors for disease potential. The 'traits' that Diaz and Madin used are summarized in Table 1.3.

Table 1.3 The nine coral 'traits' and respective attributes used by Diaz and Madin (2011) to identify which coral traits were the greatest predictors of a corals susceptibility to disease.

Trait	**Attribute type**	**Attributes**	**Source**
Characteristic local abundance	Categorical	Common Uncommon	1,2
Corallite size	Unspecified	Unspecified	1,4-6
Wave exposure	Categorical	Protected Exposed Broad (protected and exposed)	1
Preferred water clarity	Categorical	Turbid Clear Both	1
Geographic range	Continuous	Area	1
Colony growth form	Categorical	Solitary Encrusting Massive Columnar Foliaceous Digitate Branching Tabulate Corymbose	1,3
Shallowest depth found	Unspecified	Unspecified	2
Reproductive mode	Categorical	Brooder Spawner	7
Number of predatory species	Unspecified	Unspecified	8

[1]Veron and Stafford-Smith, 2002; [2]Carpenter et al., 2008; [3]Wallace, 1999; [4]Veron and Pichon, 1976; [5]Veron and Pichon, 1980; [6]Veron et al, 1977; [7]Baird et al., 2009; [8]Diaz and Madin, 2011

In trait-based ecology there is a growing consensus that the term 'trait' should only be used to refer to "features measurable at the individual level, without reference to the environment or any other level of organization" (Violle et al., 2007). Using this trait definition Diaz and Madin use only three true coral traits: corallite size, colony growth form, and reproductive mode. Diaz and Madin use the term 'trait' for characteristic local abundance, wave exposure preference, preferred water clarity, and shallowest depth. These distribution patterns are really reflections of a corals niche, which in turn is determined by the overall individual fitness of the coral, which in turn is determined by traits. The number of predatory species that a coral

has is also not a trait since its measurement relies on the presence of a predator and can therefore not be measured at the individual level without reference to its environment. The 'palatability' of a coral however is a true trait since it relies on species-level measurable attributes such as corallite width, cynidae type, tentacle length etc. Finally the disease potential is not in itself a trait since it was calculated entirely using traits. Clear definitions of what are and are not traits are needed when applying trait-based ecology to coral reefs.

Another environmental filtering event for corals are warming events. Riegl and Purkis (2009) modelled the persistence of six specific response groups to repeat bleaching events in 1996, 1998, an 2002 which caused mass mortality at two study sites in the Arabian/Persian gulf. While they referred to their groups as both 'guilds' and 'functional groups', I would argue that a more useful term here would be 'specific response group' since the intent was to examine how these species groups responded to a specific stressor (warming events). Coral species were sorted into 6 groups based on genera (*Acropora*, faviids, and *Porites*) and life stage/size (small, large).

Quantitative species-specific traits were not used to define the Riegl and Purkis six groups; instead the groups were identified using genus level growth rates and percentage coverage data for corals from 1995 when the system had presumably reached climax. As coral trait data is compiled and trait-based methodology becomes more commonplace in coral ecology, response groups should be defined using the traits they possess and then validated by observing community composition before and after filtering events rather than using field observation to define the groups and then making assumptions about the traits that define the groups. This in turn will eventually allow us to predict reef responses to stress events based on traits alone.

Storm events are also environmental filters, which coral response groups can, or cannot, pass through. Different mortality levels were found for different coral morphologies after the occurrence of the 1967 cyclones on the Heron Island reef (Hughes and Connell, 1999). The morphology groups found to be the most storm resistant in decreasing order were: massive species, encrusting species, bushy species and finally tabular species. Using additional coral traits such as skeletal density,

asexual reproduction by fragmentation, and a more detailed description of morphology (such as surface to volume ratio) would aid in refining the storm response groups further.

It is important to remember that different environmental filter events (stressors) may be operating simultaneously, or in the case of pulse events, at different frequencies. Therefore simply identifying a single response group does not allow prediction of future reef coral compositions. Response groups to a plethora of filters must be identified and their interactions with one another studied. This is a key future research area as the size and frequency of stress events on reefs increase.

1.4.2.7. The problem with coral colony morphology as a functional group

Colony morphology is a species-specific trait that influences a number of key processes; and is relatively easy to record. Because of this it has become a key trait in the functional classification of corals. When using colony morphology for functional classification it is important to 1.) clearly state the particular ecosystem function, ecosystem process, or resource utilization that the functional groups or guilds relate to, 2.) consider how the inter-specific and intra-specific variability of morphology along environmental gradients impacts upon groupings. The plasticity of colony morphology must be considered when grouping, because some species exhibit high morphological variability along environmental gradients while others do not. Therefore it is important to state if the group is useful in just one particular set of environmental conditions or if it can be applied across several.

1.4.3. Modelling species interactions using traits

As organism density increases, certain competitive traits become more important; in other words, the importance of some traits is density dependent. For example coral sweeper tentacles may not have much importance at low densities but at high densities they can become very important to survival (Sheppard, 1985). McGill (2006) suggested that biotic interactions such as competition are best treated as a "milieu or biotic background with which an organism interacts." He calls this the

'interaction milieu'. He goes on to suggest that competition can best be conceptualized using frequency-dependent game-theoretic models in which an invader (i.e. a coral recruit) must 'play the field' (Faslter and Westoby, 2003) of competition.

Langmead and Sheppard (2004) created a spatially explicit model of coral community dynamics. Their model represented a homogenous plot on a Caribbean fore-reef with 10 coral species. The model, which was based around a cellular automaton, can be conceptualized as a 300 x 300 cell chessboard. The occupancy of a cell by a 'player' (coral polyp) at each time-step was determined by its four immediate neighbours (Von Neuman neighbourhood) and pre-set interaction rules between species based on a competitive hierarchy. A coral polyp could only 'grow' into adjacent cells if that cell was either unoccupied or occupied by a coral species that was competitively subordinate. The competitive ranking of species was based on field surveys of aggressive capacity.

The construction of aggressive hierarchies in coral ecology is often based on in situ or aquarium observation of coral species' ability to overgrow one another (Lang, 1971, 1973, Sheppard, 1980, Logan, 1984, Sheppard, 1985, 1988). Directly relating coral species-level behavioural traits (i.e. presence of sweeper tentacle, sweeper polyps, histological responses, extension of digestive mesenterial filaments) and physiological traits (cnidom complements, toxicity etc.) to overall aggressive ability would eliminate the need for extensive competitive hierarchies. This would have the advantage of transferability as traits could determine which coral will 'win' in any species-species interaction thereby eliminating the need to recreate a competitive hierarchy for each system studied. However, such traits are difficult to obtain and use for several reasons (discussed later) and therefore aggressive hierarchies may well be the best option.

1.4.4. Relating coral traits to environmental variables

1.4.4.1. Importance of linking traits to environmental variables

Relating traits to environmental variables is key to creating better predictive models of how ecosystems will respond under changing environmental scenarios. Keddy (1992) suggested general predictive models could be constructed using assembly and response rules (which could be derived from understanding how traits link to environment) in addition to the following datasets: 1) the total species pool for a region, 2) the traits of these species and 3) prevailing environmental conditions at a site. The need for the development of such predictive models has been reemphasized as the realities of rapid and major environmental changes (such as climate change) raise serious questions about how communities and ecosystem functioning will respond (i.e. Thuiller, 2007). Predictive trait-based models for how species will respond to changes in the environment have already been undertaken for British butterfly populations' response to climate change (Diamond et al., 2011), bee population responses to environmental disturbances (Williams et al., 2010), and forest community responses to human disturbances (Mabry and Fraterrigo, 2009). An extensive framework for advancing trait-based prediction theory has recently been suggested (Webb et al., 2010).

It is generally observable in nature that organismal traits relate to the habitats in which they are commonly found. It has been suggested that habitat acts as a template upon which evolution then forges a set of characteristic traits (Southwood, 1977, 1988, Statzner and Resh, 1994). Establishing clearly the traits that individual species posses and how they relate to their fitness under particular sets of environmental conditions allows for better forecasting of extinction risk under different environmental scenarios thereby identifying species in need of priority protection.

Finally, relating species traits to environment variables has proved useful for predicting the invasive potential of foreign plant species (Thuiller et al., 2006, Whitney and Gabler, 2008, Van Kleunen et al., 2010). Such methodological approaches could prove highly useful in coral reef ecology as invasive introductions increase (i.e. lionfish in the Caribbean).

1.4.4.2. Historical overview of methods for linking traits to environment

That organisms 'prefer' a particular set of environmental conditions and are therefore only found in certain locations is a central in both Grinnellian (1917) and Hutchinsonian (1957) niche theory. While niche theory provides a useful underlying theoretical framework, it falls short in answering the question: what specific species traits determine their location within an ecosystem? The problem of relating species traits to the habitat conditions in which they are found is often referred to as 'the fourth corner problem' referring to the matrix formulation Legendre et al. (1997) used to solve it (see Figure 1.5). Coincidentally, the test case that motivated Legendre et al.'s study was relating 5 coral reef fish traits (feeding habits, ecological category, size class of adults, egg type, and activity rhythm) to 3 reef habitat variables (distance from shore, water depth, and percent substrate cover at each site).

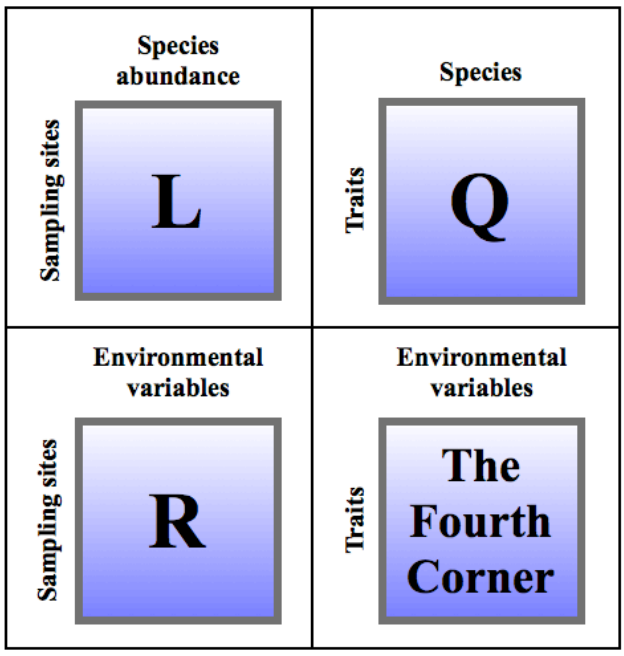


Figure 1.5 Graphical representation of the fourth corner problem. Ecologists often generate tables L (Species x Sampling sites), Q (Species x Traits), and R (Sampling sites x environmental variables). The challenge of relating environmental variables to traits is often referred to as the fourth corner problem due to the matrix formulation used to solve the problem (Legendre et al., 1997).

1.4.4.3. Statistical techniques

A number of statistical techniques have been developed to solve the 'fourth corner problem'. Since ecological communities contain multiple species with numerous quantitative and qualitative traits distributed in habitats involving a plethora of environmental conditions, statistical techniques from the field of multivariate statistics are commonly used. Here I give a brief overview of the multivariate statistical techniques developed to solve the problem of linking traits to environment.

One statistical methodology, first introduced and detailed by Dolédec et al. (1996), is a multivariate ordination method that can be used to link species traits to environmental factors and is commonly known as RLQ ordination. This type of ordination aims to investigate the relationship between table R (Sampling sites x environmental variables) and Q (Species x Traits) via a third table L (Species x Sampling sites). RLQ methodology has recently been extended to include both spatial coordinates and phylogenetic variables with script for analysis made freely available in R (Pavoine et al., 2011). Both RLQ and its recent extension are highly applicable within conservation management; both methods can be used to monitor and predict how changes in anthropogenic pressures will influence community structure in terms of traits and therefore function (see for example Ribera et al.).

1.5. Conclusion

I have reviewed the benefits of incorporating trait-based approaches into coral reef ecology, which may include: 1) the ability to link species to ecosystem properties thereby gaining clearer insight into how species and trait diversity relate to ecosystem stability and the continued provision of ecosystem services over time; 2) how species and trait diversity influences the total output of ecosystem processes (i.e. biomass production); 3) how traits may provide an insight into the underlying mechanisms of coral reef phase shifts; 4) the ability to predict future species assemblages under different environmental scenarios using traits; 5) how trait ecology can aid in better placement of MPAs.

I then briefly reviewed the four main methodological trait-based approaches that are currently available: 1) trait indices, 2) functional classification, 3) modelling species interactions, and 4) linking traits to environment. Within this framework I also reviewed any coral-based studies conducted in these four methodological areas to date.

1.6. Aims of the study

The overarching aim of the study is to test if quantifying coral life-history traits can provide useful information above and beyond that gleaned from species composition data alone. This is done via several sub-aims.

- Conduct an extensive literature review to examine what coral life-history traits are suitable and available for use in trait-based studies (Chapter Two).

- Develop a methodology for translating coral species composition into trait-combination composition that can handle species identification uncertainty for the genera *Acropora* and *Montipora* (Chapter Four).

- Test if emergent coral functional groups can be identified for the corals present in SW Madagascar with the trait data currently available (Chapter Five).

- Test if trait-based measures of site similarity provides non-redundant information when used in combination with species-based similarity measures (Chapters Six and Seven).

1.6.1. Outline of chapters

In Chapter Two morphological, behavioural, physiological, phenological and coral larval life-history traits are reviewed. The species-level data availability for each trait is discussed along with its relationship to ecosystem processes.

In Chapter Three the three study regions and 68 reefs surveyed are presented along with the major environmental forcing factors in the region. In addition the major reef types in found in SW Madgascar are presented.

In Chapter Four the field methods used to collect data, the image and gps processing workflow, database structure are discussed. Also, the sampling protocol is present along with tests for sampling bias. Finally, the major coral species clusters are presented along with the trait similarity of species within the clusters.

In Chapter Five the species present in SW Madagascar are tested for the presence of emergent groups.

In Chapter Six a new trait-based similarity coefficient (*Tsim*) is presented and its performance in relation to a species-based based similarity coefficient (*Renkonen similarity*) is demonstrated.

In Chapter Seven ordinations of reef sites using species-based based similarity coefficient (*Renkonen similarity*) are compared to ordinations of reef sites using trait-based similarity coefficient (*Tsim*). The implications of findings are discussed.

Chapter Eight provides a conclusion of results and a general discussion on the implications of the findings. Suggestions for how to move trait-based ecology forward in coral reef ecology are presented.

2.
Scleractinian life-history traits

2.1. Introduction

According to a recent review by Harrison (2011) there are currently at least 900 extant hermatypic *Scleractinian* coral species. Here I discuss the species-level traits of these corals. I define each trait, recommend measurement units, discuss known trait plasticity, and note data sources. Traits are summarized in Table 2.1 to Table 2.4 and are organized as morphological, behavioural, physiological, phenological and larval traits. For convenience I suggest units of measurement for each trait, and give its data availability status. Individual traits are discussed below.

2.2. Aims

1. To identify which *Scleractinian* life-history traits are appropriate for incorporation into trait-based studies.
2. To identify which *Scleractinian* traits have sufficient data-availability to permit this.
3. To review the relationship between life-history traits and individual fitness

Table 2.1 Schema of coral morphological traits

		Traits	Attribute example*	Advice	Section
Morphology	Colony level	Colony formation	categorical (i.e. colonial)	use	2.3.1.1.
		Colony morphology	categorical (i.e. massive)	use	2.3.1.2.
		Surface index	continuous (i.e. 3.2 NB unit-less)	use with caution	2.3.1.3.
		Attachment to reef	categorical (i.e. facultative free-living)	use	2.3.1.4.
		Colony growth strategy	categorical (i.e. determinate)	use	2.3.1.5.
		Maximum colony size	continuous (i.e. 95 cm diameter)	use	2.3.1.6.
	Corallite level	Corallite form	categorical (i.e. plocoid)	use	2.3.2.1
		Corallite spacing	categorical (i.e. widely spaced)	use	2.3.2.2.
		Corallite size	continuous (i.e. 2.6 mm diameter)	use	2.3.2.3.
	Soft tissue level	Tentacle length	continuous (i.e. 13.5 mm)	use	2.3.3.1.
		Tentacle crown surface area	continuous (i.e. 1.2 cm^2)	data paucity	2.3.3.2.
		Polyp diameter	continuous (i.e. 2 mm)	data paucity	2.3.3.3.
		Polyp integration	categorical (i.e. high)	use with caution	2.3.3.4.
		Polyp dimorphism	categorical (i.e. radial corallites)	use	2.3.3.5.
		Polyp colour	categorical (i.e. wall bright)	use	2.3.3.6.
		Cnidom profiles	NA	do not use	2.3.3.7.
		Tissue depth	continuous (i.e. 3 mm)	data paucity	2.3.3.8.
	Other	Taxonomic morphometrics	many	use	2.3.4.

*NB Continuous traits can always be translated to categorical traits (i.e. 1.3 cm becomes < 2 cm) but not vice versa.

Table 2.2 Schema of coral behavioural traits

		Traits	Attribute example*	Advice	Section
Behaviour	Feeding related	Trophic preference	continuous (i.e. CHAR‡ of 26.5 percent)	data paucity	2.4.1.1.
		Trophic plasticity	continuous (i.e. variability in CHAR)	data paucity	2.4.1.2.
		Diel tissue expansion pattern	categorical (i.e. daytime tissue projection only)	use with caution	2.4.1.3.
		Daytime tissue projection	categorical (i.e.1-5 mm)	use	2.4.1.4
	Spatial acquisition (Aggression)	Aggressive hierarchies	categorical (i.e. 34th position)	use with caution	2.4.2.1
	Sediment shedding	Active sediment shedding behaviour group	categorical (i.e. group 1B)	use with caution	2.4.3

*NB Continuous traits can always be translated to categorical traits (i.e. 1.3cm becomes < 2cm) but not vice versa.

‡Contribution of Heterotrophy to Animal Respiration

Table 2.3 Schema of coral physiological traits

		Traits	Attribute example*	Advice	Section
Physiological	Sexual reproduction	Sexuality	categorical (i.e. gonochoric)	use	2.5.1.1.
		Sexual maturity	continuous (i.e. 4 years)	don't use	2.5.1.2.
		Larval development	categorical (i.e. brooding)	use	2.5.1.3.
		Spawning behaviour	categorical (i.e. slow gamete extrusion)	use	2.5.1.4
	Asexual reproduction	Asexual reproductive mode	categorical (i.e. fragmentation)	use	2.5.2
	Growth related	Growth rates	continuous (i.e. 4 mm /yr)	don't use	2.5.3.1.
		Intra-colony budding pattern	categorical (i.e. intertentacular)	use	2.5.3.2.
	Aggression related	Toxicity	NA	don't use	2.5.4.1.
	Environmental sensitivity	Symbiont clade association	categorical (i.e. C)	use with caution	2.5.5.1.
		Hardiness	categorical (i.e. med-high susceptibility to bleaching)	use	2.5.5.2.
	Immunology related	Several potential candidate traits (see text)		data paucity	2.5.6.

*NB Continuous traits can always be translated to categorical traits (i.e. 1.3 cm becomes < 2 cm) but not vice versa.

Table 2.4 Schema of coral phenological and larval traits

		Traits	Attribute example*	Status	Section
Phenological	Spawning	Spawning schedule	categorical (i.e. May-August)	use with caution	2.6.1.
Larval biology		Larval association with symbionts	categorical (i.e. yes)	use	2.7.1.1.
		Egg/larval size	continuous (i.e. 300 um)	use with caution	2.7.1.2.
		Egg colour	categorical (i.e. pink)	use	2.7.1.3.
		larval motility	categorical (i.e. swimming)	use	2.7.1.4.
		Starvation rate	continuous (i.e. 100 days)	data paucity	2.7.2.
		Competency periods	continuous (i.e. 45 days)	data paucity	2.7.2.
		Sinking rate	continuous (i.e. 65 days)	data paucity	2.7.2.

*NB Continuous traits can always be translated to categorical traits (i.e. 1.3cm becomes < 2cm) but not vice versa.

2.3. Morphological Traits

2.3.1. Colony level traits

2.3.1.1. Colony formation

Coral polyps are either solitary or, more commonly, form colonies. Both colony formation and a solitary existence have survival advantages and disadvantages associated with it. One key advantage of colony formation is size and the possibility to share resources and stress through integration of polyps throughout the colony (see 2.3.3.4); this is not possible in solitary corals. The advantage of solitary corals is a smaller size, which confers motility enabling corals to move away from stressors, including uncovering themselves when they become buried. Colony formation is a readily observable and important trait that should be included in trait-based studies.

2.3.1.2. Colony morphology

Colony morphology is an important trait which has been shown to relate to sediment shedding ability (i.e. Stafford-Smith, 1993, Riegl, 1995), feeding success under varying flow regimes (i.e. Johnson and Sebens, 1993), internal colony light level regulation (i.e. Helmuth et al., 1997, Kaniewska et al., 2008, Kaniewska et al., 2011), reef construction (Fagerstrom, 1991), sensitivity to storm events (Hughes and Connell, 1999) and bleaching sensitivity (Wilkinson and Hodgson, 1999, Loya et al., 2001).

Colony morphology can be measured as a categorical trait and commonly has the attributes: encrusting, sub-massive, massive, tabular, laminar (horizontal), laminar (vertical), foliose, freeliving, columnar or blades, tables, corymbose, digitates, bushes, staghorn, and bottlebrush. Some coral species can exist as coralliths, which are subspheroidal, free-living growth forms commonly found in the shallow inter reef and reef flats (Glynn, 1974, Pichon, 1974, Roff, 2007). Since both bushy and submassive coralliths can form floating reefs on soft substrates and persist over time I recommend adding these colony forms to the commonplace colony morphology classifications listed above. Corals that readily fragment as a means of asexual reproduction (i.e. branching *Acropora* thickets that break off and expand onto nearby

surfaces) should not be included here as coralliths unless they have been observed as persisting spheres on floating reefs.

The plasticity of colony morphology along environmental gradients (light, water current etc.) varies between coral species (inter-specifically) and also within a species (intra-specifically). To capture inter- and intra-specific variation, all possible colony morphologies a species can assume should be included as attributes rather than just the form observed in situ. Coral morphological plasticity has recently been reviewed (Todd, 2008) and modelled using a polyp oriented approach (Merks et al., 2003, Merks et al., 2004).

2.3.1.3. Surface index

Colony morphology can be measured as a quantitative trait using surface index (hereafter SI; Dahl, 1973) which is the ratio between the surface area of the colony (in cm^2) and planar colony area (also in cm^2). SI is different from most traditional rugosity measurements since it is an area ratio rather than a length ratio. The rugosity of a coral colony is the distance ratio of the colony contour and the bisecting planar area (see Figure 2.1). While SI and rugosity are clearly related, SI is preferable since it considers the colony as a three-dimensional object.

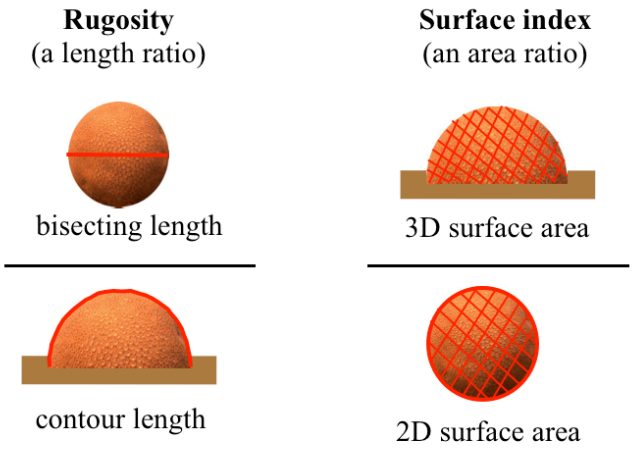


Figure 2.1 Illustration of how surface index and rugosity are calculated.

Calculating the SI requires accurate measurement of the three-dimensional surface area of the coral colony. Techniques previously used for calculating surface area in order of increasing complexity are: simple and advanced geometry, foil wrapping, wax coating, planar projection photography, computer tomography and 3-D surface reconstruction, 3-D laser scanning (Raz-Bahat et al., 2009) and X-ray computer tomography (CT) scanning. Recent studies comparing the accuracy of these techniques (Naumann et al., 2009, Veal et al., 2010) have shown that accuracy depends on the morphology of the colony; certain techniques work better for certain colony morphologies.

Creating a species-level database of SI indices for use in trait-based studies and for estimation of reef surface area could be done using the techniques listed above in combination with museum collections of coral skeletons available worldwide. As with colony morphology, SI is likely to be environmentally plastic. Therefore the plasticity of the SI of each species should be quantified by looking at skeletons collected along environmental gradients (i.e. depth, flow, light) if possible. Also, since the surface area is relative to the scale at which a coral colony is measured (colony, corallite, cell, atom etc.) and scale of measurement attainable is dependant on the technique used, care must be taken in comparing surface areas obtained by different techniques.

Building a species or genus level SI database would allow us to estimate 3-D surface area of coral tissue on a reef knowing only the 2-D coverage of each coral species (or genus) since:

$$SI = \text{3D colony surface area} \ / \ \text{2D colony surface area}$$

and,

$$\text{3D colony surface area} = \text{2D colony surface area} \times SI$$

This estimate of the biologically active surface area of a reef could be further refined by using the trait's corallite spacing and polyp surface area (discussed later) as follows.

Number of polyps on the reef = 3D colony surface area x corallite spacing

Total polyp surface area of reef = # of polyps on reef x polyp surface area

However until species-level SI data accumulates, incorporating SI indices is limited to the level of major growth forms (See Table 2.2 adapted from Holmes, 2008).

Table 2.5 Surface indices for six major types of coral colony morphology based on 158 coral skeletons from more than 25 genera and up to 75 cm in diameter (adapted from Holmes, 2008)

Colony morphology	**Surface index**
Massive	3.2
Sub-massive	5.9
Foliose	3.04
Open branching	6.16
Complex branching	6.43
Tabular	2.47

2.3.1.4. Attachment to reef

Coral attachment to reef is a trait with attributes: 1) obligate free-living corals, 2) facultative free-living corals, and 3) obligate attached corals. Obligate free-living corals are always free-living in their adult state. Facultative free-living corals are sometimes free-living in their adult form but also are commonly attached to the substrate. Obligate attached corals are never found as free-living adults. If a more detailed categorization is preferred facultative corals can further be subdivide into a) bushy coralliths, b) submassive coralliths, c) free-living plates, d) polyp balls, e) cones and f) free-living flabellomeandroid.

No Atlantic obligate free-living corals and only two Atlantic facultative free-living corals are known (*Mainicina areolata* and *Meandrina braziliensis*). In comparison, the Red Sea and Indo-pacific contains at least 52 species and 17 genera of obligate free living corals (Veron and Stafford-Smith, 2002).

Obligate free-living corals commonly have disc, dome, oval or hourglass shaped morphologies. Obligate free-living corals include all eleven genera of the fungiid family, three small hourglass shaped corals (*Heteropsammia cochlea, Heterocyathus aequicostatus*, and *Balanophyllia grandis*) and one flabello-meandroid coral (*Tachypyllia geoffroyi).*

Many faculatative free-living branching and encrusting coral species can form coralliths. Branching species form coralliths asexually via fragmentation while massive species form coralliths sexually by colonizing small pieces of rubble. Free-living plates result from detaching plates. The ability to form either coralliths or plates is a potentially important trait since it allows reefs to expand onto sandy bottoms without relying on free solid substrate (Sheppard, 1981).

While corallith formation is the most common free-living form for facultative free-living corals, other forms also occur. *Manicina areolata,* and *Cynarina lacrymalis* occasionally detach from the substrate to form free-living cones. One flabello-meandroid species, *Meandrina braziliensis*, is known to be a facultative free-living coral. Finally, *Gonipora stokesi* can develop polyp balls that detach from the main colony and roll away onto nearby soft sediments thereby acting as nuclei for the extension of reef (Sheppard, 1981). Corallith formation may be for the purpose of asexual reproduction. However, sometimes free-living coralliths do not reattach and form large extensive unattached reefs, often in shallow protected habitat (for example Glynn, 1974, Scoffin et al., 1985, Roff, 2007).

2.3.1.5. Colony growth strategy

Colony growth strategy refers to whether a coral species has determinate, indeterminate, or semi-determinate growth. Corals with determinate growth have a maximum colony size. Corals with indeterminate growth can theoretically expand their colony size indefinitely, however, in reality their size is constrained by local environmental factors. Coral species exhibiting indeterminate growth commonly form extensive stands that can dominate particular reef zones (i.e. *Acropora yongei*). Corals with semi-determinate growth have units that exhibit determinate growth (i.e.

a plate) but can form extensive stands using these units (tiers of plates). Examples, includes *A. monticulosa* (repeated rounded digitate plates), *A. polystoma* (repeated coymbose colony units), *A. valida* (repeated compact bushes or tables), and *A. vermiculata* (repeat coymbose clumps).

2.3.1.6. Maximum colony size

Most corals grow indeterminately and can therefore theoretically have an unlimited body size (reviewed by Hughes and Jackson, 1985, Sebens, 1987, Bak and Meesters, 1998). However, other corals have a typical maximum colony size. For example, solitary, free-living corals (i.e. *Fungia, Cycloseris*) have clear maximum colony sizes (for example Veron, 2000). Others such *Styllophora* spp. and *Pocillopora* spp. have clear maximum colony sizes with bushes of a characteristic shape and size. *Acropora* spp. have unclear or indeterminable maximum colony sizes, though the important table-forming species are clearly limited in size. Corals that exhibit indeterminate colony size often form extensive monostands through fragmentation. Seben (1979) argued that even for corals with indeterminate growth an optimal colony size still exists based on energetics of asexual reproduction.

The maximum colony size of a coral may increase sediment-shedding ability, resilience to bleaching, fecundity, resilience to disease, and tolerance to partial colony mortality. Connell (1973) found that mortality rates decreased sharply with increased colony size but that coral colonies with a surface area ≥ 81 cm^2 had an average mortality rate under three percent per year, suggesting a colony size refuge. Once reached the colony gains no survival advantage and therefore can invest resources into other activities such as reproduction, competition, injury repair etc. In free-living species maximum colony size also influences mobility and thereby life-strategy (Chadwick-Furman and Loya, 1992).

Thus two separate traits are needed to capture the nature of maximum colony size in corals. The first trait, colony growth type has binary categorical attributes: indeterminate or determinant growth. The second trait, maximum colony size, has continuous, numerical attributes measured as the maximum length or colony diameter that a coral species has been observed to achieve.

2.3.2. Corallite level traits

2.3.2.1. Corallite form

The trait corallite form has the attributes: plocoid, sub plocoid, ceroid, scattered, phaceloid, flabellomeandroid, submeandroid, meandroid, hydnophorid, thamnasteroid, and pachyseris type (Wood, 1983). This schema describes all *Scleractinian* corals with the exception of the mono-specific genera: *Heterocyathus, Heteropsammia, and Indophyllia*. If these species are present it is recommended that each of these species be treated as having a unique corallite form. Some have used the terms 'solitary-attached' and 'solitary-free-living' when classifying the corallite form for species in these genera, however, these terms encompass the traits of colony formation and reef attachment. Further, 'solitary-free-living is sometimes used to describe the corallite form of colonial, free-living species such as *Halomitra pileus*, which is confusing. A more useful description would be to ignore attachment and colonality in the description of corallite form, as this is covered by the trait 'reef attachment' and 'colonality' and instead classify species in the *Fungiidae* genus as having sub-meandroid corallite form if it has a axial furrow with multiple mouths (i.e. *Herpolitha weberi*), as plocoid if it has no axial furrow and only one central mouth (i.e. *Cycloseris curvata*), as scattered if it has multiple mouths and no axial furrow (i.e *Halomitra pileus*), and as having both submeandroid and scattered corallite types if a polystomatous axial furrow is present and there are also peripheral mouths outside the axial furrow (i.e *Herpolitha limax*). Because solitary colonies do not undergo intra-colony budding the classification of solitary Fungiidae species as plocoid does not affect the corallite form/intra-colony budding scheme presented later.

Corallite form is widely available in taxonomic texts and can be observed with the naked eye. Some corals can have very plastic corallite form in the same colony while others have corallite forms that are plastic along environmental gradients (i.e. Favia along depth gradients see Todd, 2008). To capture corallite plasticity in trait data all corallite types that a coral species is known to assume are included as its attributes.

Corallite form may influence the degree of small-scale self-shading a coral colony experiences, level of tissue integration (Soong and Lang, 1992) and possibly sediment rejection efficiency (Hubbard and Pocock, 1972, Hubbard, 1973, but see Bak, 1976, Stafford-Smith and Ormond, 1992).

2.3.2.2. Corallite spacing

Corallite spacing is an easily measured morphometric trait with much existing information (Veron and Stafford-Smith, 2002; and Digital Supplement 1.1.1). Trait attributes are categorical: crowded, fairly crowded, indistinct, well spaced, and widely spaced. These categories have clear definitions (i.e. 'widely spaced' is where the widest common gap between corallites is ≥ two corallite diametres).

Spacing within the colony may influence feeding. Watkins (2000) found that plotting the corallite diameter against the number of corallites per cm^2 resulted in clear niche partitioning for the corals of Silurian reefs in the Racine Formations of North America and suggested that both the diameter and the spacing may be important with regards to feeding. While a number of studies have looked at how polyp diameter relates to feeding success in modern corals I could not find any that examined the influence of corallite spacing on this. Nonetheless this is a trait that is likely to be important and its functional role should be explored further.

2.3.2.3. Corallite size

Corallite diameter and valley width are widely known characters that can either be recorded as a numerical attribute (average diameter of the corallite or valley visible on the coral skeleton) or as a categorical attribute (i.e. < 1 mm, 1-5 mm, 5-10 mm, > 15 mm; available in Digital Supplement 1.1.1; Veron and Stafford-Smith, 2002).

Stafford-Smith (1993) found that for coral species with flat tissues, a highly significant positive relationship existed between calice diameter (or valley width for meandroid species) and sediment rejection efficiency. In a related study (Stafford-Smith and Ormond, 1992) it was found that corals with calice or valley width over

about 20 mm always had a high active rejection capability for all sizes of sediment tested. They also found that maximum expansion of tissues in response to sediment was significantly greater in species with larger calice diametres than those with small calice diameter. Corallite diameter has also been suggested important in feeding (discussed later).

2.3.3. Soft tissue traits

2.3.3.1. Tentacle length

Tentacle length plays an important part in plankton capture for some coral species (discussed later). It is measured from the tentacle-oral disc attachment to the tentacle tip and can be estimated using photographs of fully expanded corals. Tentacle length is often but not consistently available in taxonomic keys. Tentacle length as a categorical trait is available for most corals (i.e. < 10 mm, 10-20 mm, > 20 mm; available in the Digital Supplement to this dissertation; Veron and Stafford-Smith, 2002)

2.3.3.2. Tentacle crown surface area

Tentacle crown surface area is likely to be important due to its influence on feeding and because it is the area through which oxygen diffusion and respiration take place. The surface area of the tentacle crown can be quantified via image analysis and advanced geometry. Estimates of individual tentacle surface areas (Levy, 2003), tentacle crown surface (Sebens et al., 1996, Sebens, 1997) and the whole expanded coral colony (Levy, 2003) have been done but are relatively uncommon. In a rare investigation of the relationship between three coral traits, Sebens (1997) found that generally tentacle length and tentacle crown surface area per unit biomass are inversely related along a gradient of corallite diameter (Figure 2.2, adapted from Sebens 1997). He suggests that a trade off exists between presenting the greatest surface area to flow (which aids in capturing prey) and having a structure that can withstand collapse in high flow conditions (short tentacles). He found that tentacle length decreases with corallite diameter for all but the smallest corallite widths (Sebens, 1997). While tentacles crown surface area appears to be important it cannot be included in trait-based studies until more data become available

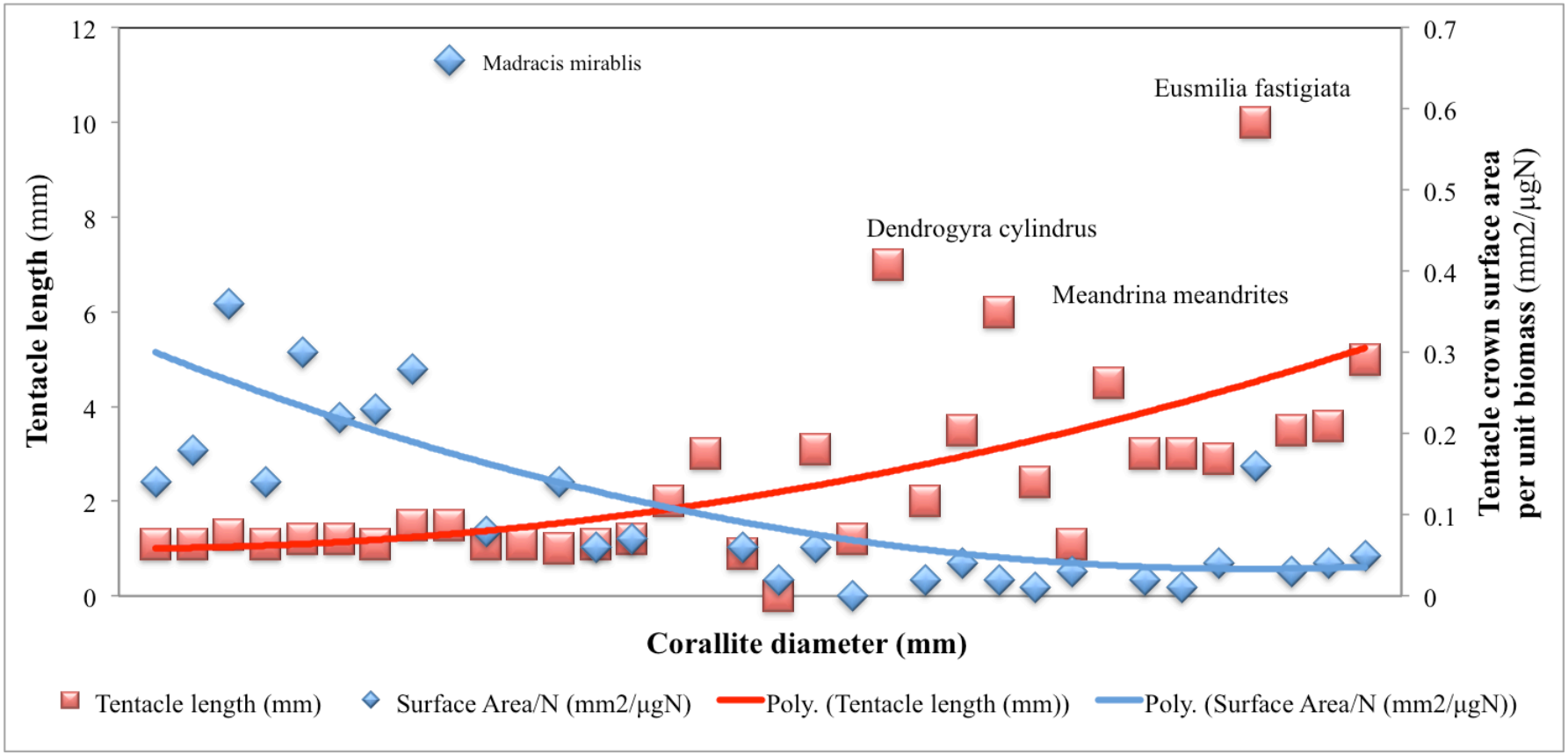


Figure 2.2 The relationship between tentacle length, tentacle crown surface area per unit biomass and corallite diameter for 35 Caribbean coral species. The data series both have 2nd order polynomial fits. Coral species are ordered along the x-axis from left to right by increasing corallite diameter. Redrawn using data from Sebens (1997).

2.3.3.3. Polyp diameter

Polyp diameter can be measured using photographs of expanded polyps and is sometimes included in literature. Polyp diameter and calice diameter are often, but wrongly, used interchangeably. While polyp and calice diametres may be interchangeably used for low lying immersed polyps, the two cannot be assumed to be equivalent for species with protruding polyps since polyps can have diametres larger than their calice diametres. This relationship has yet to be examined formally.

Polyp diameter constrains the allocation of resources to sexual reproduction; smaller polyp diametres invest a greater amount of energetic resources in sexual reproduction for hermaphroditic broadcast spawners (Leuzinger et al., 2003). The relationship between polyp size and investment in sexual reproduction for gonochoric spawners and brooding corals has yet to be examined.

2.3.3.4. Polyp integration

Corals exist along an integration gradient ranging from solitary, independent polyps to highly integrated polyps. Advantages associated with polyp integration include the ability to coordinate behaviours such as polyp retraction (Shelton, 1982), and a certain amount of differentiation of role within the colony, such as reproduction (Soong and Lang, 1992) or defence where there is relegation of development of aggressive structures to peripheral polyps of a colony.

Integration also permits reallocation of resources between polyps (Pearse and Muscatine, 1971, Taylor, 1977), and transfer to injured parts of the colony has been shown to occur in *Favia favus* (Oren et al., 2001). However, polyp integration is not a prerequisite for resource sharing. *Lobophyllia corymbosa* can transfer nutrients between isolated polyps despite the lack of a common coensarc, a process that might occur either via mucus or at night when the polyp body columns touch (Brickner, 2006).

Because form is often indicative of function, a number of traits may confer higher levels of polyp integration, such as branching morphology, dimorphic polyps, extra-tentacular budding, meandroid corallite form, common corallite walls, perforated corallite walls and well developed coenosarc tissue (Ryland and Warner, 1986, Soong and Lang, 1992). Including polyp integration as a trait can be done in three ways: 1) by including the seven morphometric traits above and being aware that they may indicate polyp integration or 2) ranking species present based on how many of the seven traits each species has (see for example Table I in Soong and Lang, 1992) or 3) creating and including a simple integration index (i.e. number of integration traits coral species possesses / total number of integration traits). I decided to use the first method as the seven integration traits have only been suggested and not demonstrated.

2.3.3.5. Polyp dimorphism

Polyp dimorphism is easily observable, and readily available in taxonomic texts with data available for most coral species (summarized for species present in Southwest Madagascar in Digital Supplement 1.1.3). Polyp dimorphism suggests functional specialization. *Scleractinian* corals exhibit two forms of polyp dimorphism: 1) presence of axial and radial corallites and 2) presence of a central larger or morphologically different polyp. Axial/radial polyp dimorphism occurs in 11 genera and 186 species, particularly *Acropora* (168 species; Veron and Stafford-Smith, 2002). This may have functional consequences: the short radial polyps and axial polyps in *Acropora palmata* and *Acropora cervicornis* are infertile which suggests that this polyp dimorphism may relate to reproductive specialization and integration within the colony (Soong and Lang, 1992).

The presence of a larger or different central corallite is found in 21 genera and 55 species (Veron and Stafford-Smith, 2002); the functionality that a central corallite may confer is currently unknown.

2.3.3.6. Polyp colour

Light management using pigments allows corals to successfully colonize a range of depths. Kaniewska (2011) recently found that micro scale (pigment-level) light regulation in the massive coral *Lobophyllia corymbosa* was greater than macro scale (colony morphology) light regulation in *Stylophora pistillata*. Microstructures such as pigmentation may thus be as important, if not more so, than macrostructures such as colony form in terms of regulating the light levels that reach their endosymbiotic algae.

In high light environments, coral pigments may protect the photosynthetic machinery of the zooxanthellae and are located in the coral tissue above endosymbionts (Salih et al., 1997). In low light conditions the coral pigments are located below the zooxanthellae (Kawaguti, 1944, Schlichter et al., 1985) and possibly enhance the availability of light by capturing short-wavelengths and re-emitting light at wavelengths suitable for photosynthesis (Schlichter et al., 1985, Schlichter et al., 1994).

Coral colour pigments are part of a family of GFP-like proteins that fluoresce under both visible and ultraviolet (UV) light (Dove et al., 2001). Four main classes of pigments have been identified and are named after the colour spectrum associated with the excitation maxima of each pigment: UV, violet, blue, and green. The colour spectrum associated with the excitation maxima of each pigment is not necessarily the same as the colour of the pigment visible to the naked eye. Both the prominence and location of pigment distribution appears to be species specific (Dove et al., 2001). The distribution of pigments can vary within a colony (i.e. the blue tips of *Acropora* spp.) and also within a polyp (i.e. the oral discs of *Blastomussa* are a different colour than the surrounding tentacles).

I recorded polyp colour simply as the colour pattern between the wall and centre of the polyp i.e. uniform dull, centre bright, wall bright, uniform bright (following Huang et al., 2009). Genera that exhibit colour patterns on a colony scale include *Acropora* where the axial corallite is often blue, pink, or lilac. To accommodate this I recorded *Acropora* species with coloured tips as having two polyp attributes: polyps

that are uniform dull and polyps that are uniform bright. Basic colour patterns can be assessed from images. Peripheral colour patterns for species in Southwest Madagascar are summarized Digital Supplement 1.1.3.

2.3.3.7. Cnidom profiles

Cnidae are structurally and functionally unique organelles found exclusively in phylum Cnidaria. Cnidae have three basic forms: nematocysts (which occur in all cnidarians), spirocysts (found only in anthozoan Subclass Hexacorallia) and ptychocysts (confined to tube anemones; hexacorallian Order Ceriantharia). These basic cnidae forms have been further subdivided based on morphological type. For example, the major nematocysts morphologies described for *Scleractinian* corals to date include: holotrich I and II, *b*-rhabdoids, *p*-rhabdoids and agaricysts which can in turn be further subdivided based on morphological details (see Pires, 1997). The nomenclature for cnidae has yet to be formally agreed upon and varies between authors causing difficulty in compiling cnidae data from multiple sources. A useful nomenclature introduced by Pires (1997) details how the structures have been referred to in other publications.

While much attention has been given to the morphological details of cnidae in the interest of use in taxonomic classification (Pires, 1997) defining the relationship between structure and function is mostly made through inference. For example, nematocysts that contain threads open at the tips (stomocnidae) are thought to deliver toxins to prey while threads with closed tips (desmonemes) are thought to be ensnaring. Holotrichs bear spines along the entire length of their threads suggested as primarily for defence. Spirocysts, which adhere to both prey and non-prey, appear to have a more general function (Mariscal and Bigger, 1974). Based on such inferences nematocysts can be grouped into four functional categories, those that: 1) pierce predator or prey and inject toxins 2) ensnare prey 3) adhere to substrate and 4) those used in defence (Kass-Simon and Scappaticci, , 2002). All such inferences have yet to be formally tested.

The aggressive ability of corals may relate to cnidom type or number. Thomason and Brown (1986) showed that the number of nematocysts per polyp was consistent with known aggression rankings for ten Indo-Pacific and Caribbean *Scleractinian* coral species. They found that aggressive proficiency of coral species was not related to calice size, number of tentacles, or number of mesenterial filaments but rather to total number of nematocysts per polyp.

Will a cnidom and/or nematocyst per polyp density database for coral species aid in trait characterisation? There remains no evolutionary context for cnidae, so results on the coral species level may be independent of genus and therefore every single coral species would need to be tested. Also, the lack of evolutionary context forces us to rely completely on our understanding of the mechanic and toxicological features that infer different levels of aggressive ability. In addition, it is unknown if nematocyst morphology is related to the type of toxin each contains.

There is little information either on the variability of the cnidom complement geographically, seasonally, or under varying environmental regimes. In order to use the cnidom complement as an index for aggression one would first have to test the stability of cnida complements across these gradients.

The nematocyst complement is most complete for anemones (Fautin, 1988) since their taxonomic classification is forced to rely on soft tissues. Despite the initial disinterest in coral cnidae, cnidom data is beginning to accumulate (for example Thomason and Brown, 1986, Pires and Pitombo, 1992, Pires, 1997, Peach and Hoegh-Guldberg, 1999, Ogawa and Nomura, 2009, Picciani et al., 2011), but different authors have used different classifications schemes. Here the classification scheme of Pires (1997) is followed. Data types available include: size, number, and distribution of cnida types in tentacle tips, sweeper tentacle tips, and mesenterial filaments (see for example Table 1 in Thomason and Brown, 1986).

In summary, cnidom complement may be a useful trait to include in trait-based analysis in the future but currently requires that data be compiled, and that the relationships between structure, function, toxicity, and taxonomy be clarified.

2.3.3.8. Tissue depth

While the skeleton of some corals may continuously increase, the soft tissue that occupies it does not increase in a simple linear way, since it is restricted to the outermost millimetres of skeleton. Measuring the depth of the living tissue is easily done by sawing or fracturing the colony and then measuring the dark band of tissue present in the outermost layer of the coral and separated from the dead skeleton by the position of dissepimental sheets (thin skeletal bulkheads see Figure 2 in Barnes and Lough, 1992). Measuring the depth of (former) living tissue thickness in dead or bleached corals is done by measuring the distance from the surface to the dissepimental sheets. Since tissue depth can be measured for dead coral a species-level database of tissue depths could be created using bleached coral skeletons in museum collections.

Tissue depth decreases under stressful conditions such as when competing with turf algae for space (for example Quan-Young and Espinoza-Avalos, 2006). This is likely due to resource allocation from tissue maintenance to structures associated with competition. It has also been found that tissue thickness can vary by location (Barnes and Lough, 1992) indicating that local environmental conditions impact upon tissue thickness. Because of this it is important when creating a tissue thickness database to indicate the local conditions under which the specimen was collected, if possible. Nonetheless a tissue thickness range could potentially be a useful trait as a measurement of tissue depth under 'normal' conditions may be an indication of how much reserve the coral has to spend in term of tissue thickness once stress events occur. Tissue thickness may be an important trait but cannot currently be incorporated into trait-based studies due to data paucity.

2.3.4. Taxononomic morphometrics

Detailed morphometric traits are readily available from taxonomic literature (Veron and Stafford-Smith, 2002) on conditions such as septae, costae, septo-costae, paliform structures, extra thecal structures, columella, etc. These may well be important in terms of improving individual fitness under different environmental

conditions, but no studies to date have tested this and therefore there is little to discuss. The detailed morphometric trait descriptions in the electronic taxonomic key Coral ID (Veron and Stafford-Smith, 2002) have been summarized in Appendix One for reference. In order to facilitate the use of Coral ID trait data with the programming tools presented in later chapters the Coral ID trait data (including morphometric trait data) was converted into a .csv file, which is available as Digital Supplement 1.1.1 (all species) and 1.1.2 (species present in Southwest Madagascar only).

2.3.5. Morphological structures and heterotrophic feeding success

Several of the traits in the previous sections, namely: colony morphology, polyp size, and tentacle length have been implicated as contributing to heterotrophic feeding ability. Due to the amount of attention these trait-function relationships have received I address these here in this separate section.

Porter (1976) suggested that species with low surface to volume ratios (i.e. sub-massive and encrusting growth forms) and large polyps are more adapted to capturing zooplankton than species with large surface to volume ratios (i.e. branching coral species) and small polyps, which would be better at capturing light. It was suggested (Houlbreque and Ferrier-Pages, 2009) that a number of studies from both the Caribbean (Sebens et al., 1996, Sebens et al., 1998) and the Gulf of Panama (Palardy et al. 2005, 2006) contradict Porter's model. Combined, these studies looked at eight species of coral (*Porites lobata, Porites compressa, Montipora capitata, Pavona clavus, Pavona gigantean, Pocillopora damicornis, Madracis mirabilis, and Montastrea cavernosa*). Only one of these corals (*M. cavernosa*) has a large calice width while the remaining coral species have small calice widths. Therefore use of a broader range of calice widths, morphologies, and tentacle lengths would be useful to examine whether their morphology is specialized for either auto- or heterotrophy.

Abelson et al. (1993) proposed a model where species with a high slenderness ratio (SR -height to width ratio of the body) are mainly suspension feeders while those

with a low SR are coarse particle or bedload feeders. Vertical flow velocity gradients and the resulting distribution of food particles across the colony have been considered (Jumars and Nowell, 1984, Muschenheim, 1987).
It has been suggested that for a fixed biomass it is energetically more efficient to have many small polyps rather than a few large ones (Sebens, 1979). This is because small corallites with short tentacles spread their biomass over a larger surface area than do large corallites with large polyps thereby maximizing the feeding surface per biomass unit.

It has been observed that the size and taxonomy of ingested zooplankton do not vary between coral species regardless of coral species, bleaching status, depth, polyp size, and coral colony morphology (Sebens et al., 1996, Palardy et al., 2005, 2006, Palardy et al., 2008) supporting the hypothesis that coral species do not exhibit an innate difference in their ability to capture different assemblages or size classes of zooplankton.

Sebens et al. (1996) found no difference between the selectivity of prey between *Madracis mirablis* (small polyps, branching morphology, high S:V ratio) and *Montastrea cavernosa* (large polyps, massive morphology, low S:V ratio). However the probability of capturing a plankter as it passes through the crown was 36 times higher in *M. mirablis* (branching, small polyps) than for *M. cavernosa* (sub-massive, larger polyps). Both species were selective towards larger prey such as decapod shrimp, polychaetes, chaetognaths, isopods, and crab zoea rather than the small more abundance and more nimble copepods. They noted that on nights with greater flow speed, the capture rate for smaller prey (copepods) was greater for both species. This is likely due to higher flow speeds disabling the escape abilities of copepods; they simply get pushed into the coral tentacles by the flow. Interestingly, there were major differences in the size distribution of prey depending on the sample date (Figure 7, Sebens et al., 1996) which may be reflective of differences in flow on different days.

The importance of particular morphological structures to heterotrophic feeding may vary depending on flow speed, particle size, density, size and spacing of filtering structures (Rubenstein and Koehl, 1977, LaBarbera, 1984, Shimeta and Jumars,

1991, Riisgard and Larsen, 2010). Dense particles deviate from the streamlines around tentacles due to a physical process called inertial impaction and which also is likely an important mechanism for capture of larger particles at flow velocities around 0.5 s^{-1} (Sebens and Koehl, 1984). In low flow conditions, such as in lagoons or in deep water, gravitational deposition of particles can be more important (Sebens and Johnson, 1991, Abelson et al., 1993).

Johnson and Sebens (1993) examined how flow, colony orientation, and position of polyps in a colony relate to feeding success and found feeding rates and flow rates to be inversely related. They also showed that corals with tentacles of different mean length feed successfully at different flow rates.

2.4. Behavioural traits

2.4.1. Feeding related behavioural traits

Nutrient acquisition is critical and corals exhibit exceptionally diverse multitrophic pathways (reviewed by Goreau et al., 1971, Muscatine, 1973, Houlbreque and Ferrier-Pages, 2009). Three species-level behavioural traits central to nutrient acquisition are: 1) trophic preference 2) the ability to increase heterotrophic feeding when conditions for autotrophy are suboptimal and 3) the diel patterns of tentacle and tissue expansion.

2.4.1.1. Trophic preference

While light has long been thought to be the main limiting factor for coral growth, heterotrophy limits growth also; it stimulates zooxanthellae densities, pigmentation, photosynthesis, and growth in *Stylophora pistillata* (Ferrier-Pages et al., 2003, Houlbreque et al., 2003, Houlbreque et al., 2004), growth rate and photosynthetic capacity in *Seriatopora caliendrum,* and growth but not photosynthetic activity in *Pocillopora damicornis* (Osinga et al., 2011). The importance of heterotrophic feeding to coral physiology has recently been reviewed (Houlbreque and Ferrier-Pages, 2009).

Preferred trophic mode is species specific in corals and is a key trait in shaping their fundamental niche (Anthony and Connolly, 2004). Some coral species such as those in the genus *Tubastrea* rely only on heterotrophic feeding while others such as *Stylophora pistilillata* are highly adapted to bright light conditions of shallow waters. It is useful to think of coral species as existing on a continuum from 100 percent heterotrophic to nearly 100 percent photoautotrophic (however, no exclusively photoautotrophic species are known). Position on this scale can be measured as the percentage of heterotrophically acquired carbon (H_C) relative to total daily carbon required by the coral (R_C). This has been referred to as the contribution of heterotrophy to animal respiration (hereafter CHAR; Grottoli et al., 2006).

A similar measure, contribution of zooxanthellae to animal respiration (CZAR; Muscatine et al., 1981, Muscatine et al., 1983) could alternatively be used.

Approximating feeding rates (required for calculating CHAR) for individual coral species is a tedious and labour intensive exercise. To date CHAR has only been calculated for three coral species. Due to the effort required it is unlikely that a feeding rate database can be constructed on a large scale for *Scleractinian* corals using traditional methods. However, efforts have been made to develop stable isotope proxies for feeding (Felis et al., 1998, Grottoli, 1999, Grottoli and Wellington, 1999, Grottoli, 2002, Rodrigues and Grottoli, 2006) and it has been found that the stable isotope signature δ13C is a good isotope proxy. It should be noted that for corals that are heavily bleached the relationship between δ13C and CHAR becomes more complex (Grottoli et al., 2004, Rodrigues and Grottoli, 2006) and the only reliable method for quantifying feeding rates for bleached corals is through direct measurement.

While trophic preference cannot currently be incorporated into trait-based studies it represents an area of important future research.

2.4.1.2. Trophic plasticity

Some corals can adjust their trophic mode to optimize nutrient acquisition under different conditions. This may occur along depth (Grottoli, 1999, Palardy et al., 2005, Palardy et al., 2008) and turbidity gradients (Anthony, 2000). This capacity may confer resilience during bleaching events since vital nutrients can still be obtained in absense of *Symbionium*. Grottolli et al. (2006) observed slight bleaching induced upregulation in *Porites compressa* (CHAR 16.84 percent to 25.76 percent) and *Porites lobata* (CHAR 24.85 percent to 39.63 percent) with large upregulation occurring in *Montipora capitata* (CHAR 11.91 percent to 78.08 percent).

While trophic plasticity is an important trait, currently data paucity limits its use.

2.4.1.3. Diel tissue expansion pattern

Corals exhibit several diel expansion/contraction patterns (Kawaguti, 1954, Abel, 1963, Porter, 1974, Lewis and Price, 1975, Lasker, 1979). Corals either expand their tentacles only at night, only during the day, or continuously (Eguchi, 1936, Abe, 1939, Kawaguti, 1954, Porter, 1974, Lewis and Price, 1975, Sweeney, 1976). Nocturnal tissue expansion facilitates heterotrophic feeding during greatest plankton densities while daytime expansion increases the surface area available for solute exchange thereby aiding in zooxanthellate generation of sugars (Levy et al., 2006). Continuously expanded corals use two main strategies for effective light harvest: 1) they have dense algal populations (i.e. *Goniopora lobata*) or 2) short tentacles that do not scatter available light or self-shade (i.e. *Stylophora pistillata*; Levy, 2003).

Some corals feed primarily through use of mucus nets (Lewis and Price, 1975) while others have no tentacles, such as *Mycetophylia reesi,* and rely entirely on mucus entrapment for heterotrophic feeding (Goldberg, 2002). Corals that feed using mucus nets and entrapment must still expand their tissues to do so. Also, corals contract their tentacles and tissues when they cannot feed and thus expansion must have an associated cost or risk (Porter, 1974, Sebens and DeRiemer, 1977). Therefore one can conclude that the diel pattern of tentacle and tissue expansion contraction is an

important trait for all corals regardless of mode of feeding and should be included in coral trait-based studies.

Diel expansion data for most corals are available via the electronic taxonomic key Coral ID and also as a .csv file (see Digital Supplement 1.1.1). It should be noted that in addition to light, water flow and the presence of prey also influence the expansion of coral polyps (Levy et al., 2001). Since taxonomic references do not commonly state flow or nutrient conditions under which a species expands or contracts, taxonomic tissue expansion data should be considered general, as it does not necessarily capture the expansion/contraction behaviour in more extreme environmental conditions.

2.4.1.4. Daytime tissue projection

The distance that corals expand their tissues (tentacles, mantles, and vesicles) is highly variable and has implications for active feeding using tentacles and mucus nets to capture plankter. Tissue projection also has implications for the productivity of symbionts in coral tissues as discussed above. Daytime tissue projection is available through the electronic taxonomic guide Coral ID (Veron and Stafford-Smith, 2002).

2.4.2. Aggression related behavioural traits

It is estimated that less than 1.2 percent of the world's continental shelf area, and only around 0.09 percent of the world's oceans meet the habitat requirements of shallow warm-water corals (Spalding et al., 2001). Such requirements included the presence of firm substrate on which coral larvae can settle and develop into coral polyps. In addition, such substrate must be located in a position that allows the coral to obtain enough light for the zooxanthellae to produce energy (reviewed by Stambler, 2011) and enough water movement for zooplankton and particulate matter to be passed over the polyp for heterotrophic feeding (recently reviewed by Houlbreque and Ferrier-Pages, 2009). For the small amount of free substrate that meets these requirements, competition is intense and has provided the evolutionary

pressure for a number of aggressive behaviours and structures to develop. *Scleractinian* spatial competition has recently been reviewed (Chadwick and Morrow, 2011) addressing the 20 year gap since the previous review by Lang and Chornesky (1990).

Using behaviours such as this is difficult because their development is dependent on the competitive mileu (i.e. distance and identities of neighbours). Gradients of competitive mileu, unlike abiotic environmental gradients (i.e. light), are difficult to quantify (what would the unit be?). Without a measurement for gradient, a gradient dependant trait cannot be measured.

Further complicating the matter, the success of different aggressive behaviours vary along flow gradients. Genin and Karp (1994) observed that the sweeper tentacles of *Galaxea fasicularis* were ineffective in high flow conditions. It is likely that in high flow conditions a fast growth rate and the resulting overgrowth of neighbours is a more successful aggression strategy than sweeper tentacles/polyp formation, mesenterial filament extraction and allelopathy.

Finally, while aggressive behaviour is important, the cnidom profiles (discussed earlier) that corals posses are linked to the effectiveness of some forms of interaction. In other words, a coral can position itself for attack on a neighbour, but if it lacks 'fire power' in terms of cnidae the importance of its behaviour is irrelevant.

One alternative, although fraught with its own set of difficulties, is to use aggressive hierarchies to translate aggressive behaviour/ability into a trait.

2.4.2.1. Aggressive hierarchies

A corals competitive ability is always relative to its opponent. For a particular pair of coral species, for any given mechanism one coral will usually be consistently dominant over the other (Sheppard, 1979). Because of this, historically field surveys of coral competition have focused on developing 'networks of competitive dominance'. Using the position of a coral in such hierarchies as a trait is labour

intensive, as it requires knowledge of the competitive outcomes between all *Scleractinian* species on a reef. Even a simple system with 30 coral species results in 435 interactions to record. Then again, all such interactions do not naturally occur since particular corals are restricted to certain habitats, thus, the number of naturally occurring interactions will always be less than the total number of possible interactions. Also it is important to consider interactions at more than one time-point in order to record competitive interaction reversals (reviewed by Lang and Chonesky, 1990, Chadwick-Furman and Rinkevich, 1994, Langmead and Chadwick-Furman, 1999).

Compiling coral interaction data into a large-scale interaction table (database) could be useful as a competitive index such as that used by Dai (1990) could then be applied. Dai calculated aggressive index (CI) as the number of wins minus the number of losses divided by the total number of interactions and CI can therefore range from -1 for corals that lose all interactions and +1 for corals that win all interactions. CI could be used as a numerical trait or used to create a categorical trait (i.e. high, med, low). Alternatively, similarity measures such as the Gower similarity coefficient could be applied and species with similar patterns of wins and losses could be grouped into aggression categories.

2.4.3. Active sediment rejection behaviour group

Active sediment rejection behaviour for a wide range of Indo-Pacific (Stafford-Smith and Ormond, 1992) and Caribbean species (Hubbard and Pocock, 1972, Bak, 1976) has been observed (see also review by Rogers, 1990). Data are commonly recorded as qualitative observations of coral behaviour in response to covering by sedimentation of varying sizes. The active rejection behaviours include: ingestion, ciliary transport of particles, mucus production, tissue expansion, tentacle manipulation of particles, extrusion of mesenteries, and pulsing of tissues. While these studies are interesting and important, the observational data they contain is difficult to summarize and translate into traits due to different qualitative observational scales.

Despite this, using the results from a single large-scale study and translating the observations into a ranking of active sediment rejection ability may still be appropriate. Stafford-Smith and Ormond (1992) quantified the sediment shedding behaviours for 42 species from 31 genera with wide Indo-Pacific distributions. Based on seven active rejection behaviours corals were sub-divided into seven groups of active-rejection capability. With the exception of some *Faviidae* species, sediment rejection mechanisms were consistent for both conspecifics and congeners. Therefore the results from this study could cautiously be used to classify the active sediment rejection ability of other family members of similar morphologies. Sediment rejection data for the 42 species is available in Digital Supplement 1.1.4.

2.5. Physiological traits

2.5.1. Sexual reproductive traits

Reproductive trait information (mainly sexuality and larval development classifications) is available for at least 444 species (Harrison, 2011) and has been compiled into a database by Baird et al. (see Supplemental Appendix I in Baird et al., 2009). An updated version of this database is available in Digital Supplement 1.1.5. Kerr (2011) offers a useful discussion on the coevolution of sexual systems and reproductive mode in corals.

2.5.1.1. Sexuality

Corals have two sexual systems: 1) polyp hermaphroditism where each polyp is both male and female and can simultaneously produce both eggs and sperm within a complete breeding cycle and 2) gonochoric polyps where all polyps in a colony are either exclusively female or male and thus the colony can produce only eggs or sperm throughout their lifetime (dioecious). The consistency of sexuality within the monophyletic molecular clades of Fukami et al. (2008) is high, thus inferences about species sexuality for which data is missing can reasonably be made.

Exceptions to the hermaphroditic/gonochoric dichotomy exist. Protandrous simultaneous hermaphroditic colonies are male at small sizes and then become

simultaneous hermaphrodites (male and female) once they reach a species-specific characteristic size. This allows delayed allocation of energy to expensive female functions thereby giving the coral an energetic advantage as a small coral. This has been observed in *Stylophora pistillata* (Rinkevich and Loya, 1979). Sequential protandrous hermaphrodites are solely male when small and solely female when larger and have been observed in at least 4 solitary fungiid species (Kramarsky-Winter and Loya, 1998, Loya and Sakai, 2008). One fungiid species, *Ctenactis echinata* can undergo a bidirectional sex change which is thought to give it a energetic advantage under particular environmental constraints (Loya and Sakai, 2008). *Diplostrea heliopora* and *Cladopsammia rolandi* are known to have mixed breeding with male polyps and female polyps occurring within the same colony. *Galaxea fasicularis* has female colonies, which release pinkish-red eggs, and hermaphroditic colonies, which release sperm and lipid-filled white eggs that cannot undergo fertilization. The white eggs and sperm are released as a bundle. The white eggs function to lift the sperm to the surface where they can fertilize the pigmented eggs (Harrison, 1989). This sexual mode is termed 'pseudo-gynodioecious, but could for practical purposes be considered simply as gonochoric. Finally, some gonochoric species populations exhibit low-levels of hermaphroditism (Delvoye, 1988, Soong, Glynn et al., 1994, Glynn et al., 1996), and have been called 'stable gonochores' (Giese and Pearse, 1974).

Thus coral sexuality can be considered a binary trait (hermaphroditic or gonochoric) by considering only the adult sexuality of a coral (as is done in this study). Under this scheme protandrous simultaneous hermaphrodites are simply hermaphrodites while sequential protandrous hermaphrodites, pseudo-gynodioecious, stable gonochores are just classified as gonochoric (see Table 2.6). The mixed breeding system found in *D. heliopora* and *C. rolandi* are neither gonochoric nor hermaphroditic and represent a unique sexual system. If either of these species is present, sexuality should be considered a trait with tertiary attributes.

Table 2.6 Exceptions to the hermaphroditic/gonochoric dichotomy and how they are translated into sexual reproductive trait attributes in this study.

Sexuality type	Description	Examples	Trait attributes used
Protandrous simultaneous hermaphrodites	colonies are male at small sizes and then become simultaneous hermaphrodites (male and female) once they reach a species-specific characteristic size	*Stylophora pistillata* (Rinkevich and Loya, 1979)	Hermaphrodite
Sequential protandrous hermaphrodites	solely male when small and solely female when larger	four solitary fungiid species (Kramarsky-Winter and Loya, 1998, Loya and Sakai, 2008).	Gonochoric
Pseudo-gynodioecious	female colonies which release pinkish-red eggs and hermaphroditic colonies which release sperm and lipid-filled white eggs that cannot undergo fertilization.	*Galaxea fasicularis* (Harrison, 1989).	Gonochoric
Stable gonochores	gonochoric species populations exhibit low-levels of hermaphroditism (Delvoye, 1988, Soong, 1991, Glynn et al., 1994, Glynn et al., 1996)	Family Agariciidae (Delvoye, 1988, Glynn et al., 1996) and Poritidae (Soong, 1991, Glynn et al., 1994)	Gonochoric
Mixed breeding system	male polyps and female polyps occurring within the same colony	*Diplostrea heliopora* and *Cladopsammia rolandi*	Mixed

2.5.1.2. Sexual maturity

Sexual maturity is difficult to include in trait-based studies for three reasons: 1) paucity of data 2) sexual maturity must be measured on different scales due to species-specific limiting factors for onset of first gametogenesis (i.e. colony size, polyp size, number of polyps per colony) and 3) sequential sexuality switching in some corals confuses the concept.

Quantitative data for sexual maturity in corals are relatively rare. I could find data for only 17 Caribbean species (Szmant, 1991, Soong and Lang, 1992, Soong, 1993) and 11 Indo-pacific species (Babcock, 1984, Kojis and Quinn, 1985, Fan and Dai, 1995, Sakai, 1998).

Onset of gametogenesis for these 28 species has been recorded as: estimated age, branch length, colony diameter, polyp number, and surface area. Because of these different units of measurements it is difficult to draw general conclusions from the existing data. The difference in measurement units reflect the fact that onset of gametogenesis in some species may have multiple limiting factors. For example, the interaction between polyp age and size have been shown to influence puberty in *Goniastrea favulus* (Kojis and Quinn, 1985) while the colony size, polyp number, position and volume interact to determine sexual maturity in *Goniastrea aspera* (Sakai, 1998).

2.5.1.3. Larval development

Gametes may either be broadcast with fertilization in the water column or brooded after internal fertilization (see reviews by Harrison and Wallace, 1990, Richmond and Hunter, 1990, Harrison, 2011). Broadcast spawning is far more common (338 of 404 or around 84%; Baird et al., 2009) than brooding coral (64 of 404 or around 16%; Baird et al., 2009). While reproductive mode is more taxonomically flexible than sexuality, it is still relatively stable with 13 of 110 genera containing both spawning and brooding species. The larval development data summarized by Baird et al. (2009) is available as 'Reproductive mode' in Digital Supplement 1.1.5.

2.5.1.4. Spawning behaviour

Spawning behaviour refers to the manner with which coral species release their gametes. Babcock et al. (1986) recognized three main types of gamete release based on observation of spawning of 105 species on the GBR: slow extrusion of gametes (Type I), vigorous ejection of gametes (Type II), and passive release of gametes (Type III). While not formally tested, it is likely that spawning behaviour influences at least the initial distribution of gametes into the water column. The study by Babcock et al. represents the largest source of spawning behaviour data available. Elsewhere in the literature data is occasional and does not follow the same typology as Babcock et al. Therefore the use of spawning behaviour may be limited to regions with similar biogeographic distributions to the GBR.

2.5.2. Asexual reproductive mode

Asexual reproduction may be the dominant form in some corals. Species with slow growth rates, small adult sizes and short life expectancies are likely to favour sexual reproduction while corals with fast growth rates, large adult sizes and long life expectancies are more likely to favour asexual reproduction (Highsmith, 1982) although see growth rate caveat discussed later.

However, no coral species is known to reproduce exclusively via asexual means; even those commonly observed to reproduce via e.g. fragmentation as in *Acropora* spp. and *Fungia* are still capable of reproducing sexually. Categorising corals as primarily sexual or asexual reproducers would require measures of energetic investment in each strategy over time and no such study has been attempted to date.

Nonetheless, the mere ability to reproduce via an asexual strategy can be used as a trait. To date, five asexual reproductive traits have been identified and their presence within genera is relatively well documented:

- Asexual production of brooded planulae is known to occur in *Pocillopora damicornis* (Stoddart, 1983, Ayre and Miller, 2004), *Tubastraea coccinea, Tubastraea diaphana* (Ayre and Resing, 1986) and *Oulastrea crispata* (Nakano, 1992). Both *P. damicornis* and *O. crispata* are also sexual spawners and brooders, suggesting extreme reproductive plasticity. To my knowledge, no other coral species have been identified as asexual brooders.

- Bud shedding (anthoblast production) occurs in solitary or 'quasicolonial' corals. Asexual buds (anthoblasts) develop on both living and nearly dead specimens ('Phoenix effect'), and then the polyp detaches leaving a scar at the site of former attachment from which new polyps can grow. Detached polyps can go on to reproduce both sexually and asexually. All genera of the *Fungiidae* family (except the genera *Lithophyllon* and *Podabacia*) produce anthocauli from which anthocyathi subsequently detach (Veron and Pichon, 1980).

- Fragmentation is common in some genera such as *Acropora*. The combination of fragmentation with high growth rates can result in domination of certain reef zones, and promotes rapid recovery rates after physical disturbances. Fragmentation has been observed in species with bushy, plating, and massive colony morphologies as well as solitary corals. Species-level observations of fragmentation are well documented but remain to be summarized into a database.

- Polyp balls are the development of detached small skeletons within the large fleshy mass of tentacles, and to date has only been observed in *Goniopora stokesi.* Polyp balls are used to colonize soft substrates thereby extending the reef (Sheppard, 1981). It seems likely this trait is unique to this species.

- Under stressful conditions coral polyps can detach from their skeleton and recolonize elsewhere, this is commonly referred to as 'polyp bail out'. This mode of asexual reproduction has been observed in *Styllophora hysterix* (Sammarco, 1982) and *Pocillopora damicornis* (Richmond, 1985) and has been suggested to contribute to these species dominance of particular habitats. It remains unknown whether other species employ this method.

- Polyp expulsion is the detachment of both polyp and calice from the surrounding skeleton. It has been observed in *Oculina patagonica* and *Favia favus* in shallow waters (Kramersky-Winter et al., 1997). This mode of asexual reproduction may be very important in high disturbance areas where starting life as a juvenile rather than planulae is preferential. Until the commonality of polyp bail out and polyp expulsion is further establish these traits cannot be included in trait-based studies.

2.5.3. Growth related traits

2.5.3.1. Growth rates

As with plants, coral growth rates can be highly dependant on environmental conditions. Therefore, before incorporating growth rates into trait based studies it is vital to establish the plasticity of growth rates along environmental gradients at the species (or at least genus) level. Environmental factors known to influence coral growth rates include: temperature (Glynn and Stewart, 1973, Weber and White, 1974, Tanzil et al., 2009), light and zooplankton availability (Wellington, 1982), competition (Neudecker, 1977), flow (Nakamura and Yamasaki, 2005, Schutter et al., 2010), and sedimentation (Crabbe and Smith, 2005). Growth rates appear to be dependent on overall colony size for some corals (Vago et al., 1997) but not for

others (Kinzie and Sarmiento, 1986, Vago et al., 1997). It is likely that the relationship between colony size/age and growth rates is species specific.

A database compiling coral growth data is much needed, containing: species name, measurement unit of growth (i.e. mm or cm), the start date of observation, the end date of observation, the total number of observation days, the method of observation, the estimated annual growth rate for species, the number of specimens that the growth rate estimate is based on, the depth at which the measurement was made, the flow conditions at location of measurement, sediment regimes at location, geographic location, GPS coordinates, lab/field observations, reference, and specific notes about the data source should also made. Until such databases have been analysed and degree of plasticity firmly established, it is recommended to exclude growth rate as a trait.

2.5.3.2. Intra-colony budding pattern

Budding pattern is readily observable and is species-specific. The common terms intra-tentacular and extra-tentacular do not satisfactorily describe budding in corals where wall structure is poorly pronounced. Therefore I suggest that 'incomplete intra-tentacular budding', 'thamnasteroid-budding', and 'hydnophorid budding' be added for a total of five possible trait attributes (detailed later).

Budding pattern has a number of fitness implications for corals. Firstly, colony form is largely determined by budding pattern and growth rate. Secondly, budding pattern may influence the degree to which polyps are integrated; for example, whether polyps remain organically linked or become separated. Extra-tentacular budding results in polyps that are not functionally integrated via enterons but can maintain chemical or nervous linkage via soft tissues (Clarkson, 2009). Budding pattern has also been shown to influence reproductive maturity of daughter polyps. Sakai (1998) found that the marginal polyps of *Goniastrea aspera* that exhibited extra-tentacular budding were initially immature and far less fecund than non-marginal polyps, which exhibited intra-tentacular budding and reproductive maturity.

Particular corallite forms are bound to particular types of intra-colony budding patterns. Some corals can have multiple corallite forms and therefore multiple budding patterns, sometimes within the same colony. The budding type restriction that each corallite type confers is summarized Figure 2.3. Solitary corals, by definition, do not undergo intra-colony budding. The anthocauli budding that occurs in many freeliving members of the *Fungidae* family is considered a form of reproduction and not intra-colony budding. Freeliving colonial corals, most of which are present in the *Fungidae* family, undergo intratentacular in-complete budding resulting in an axial furrow or intra- and extra-tentacular budding outside the axial furrow.

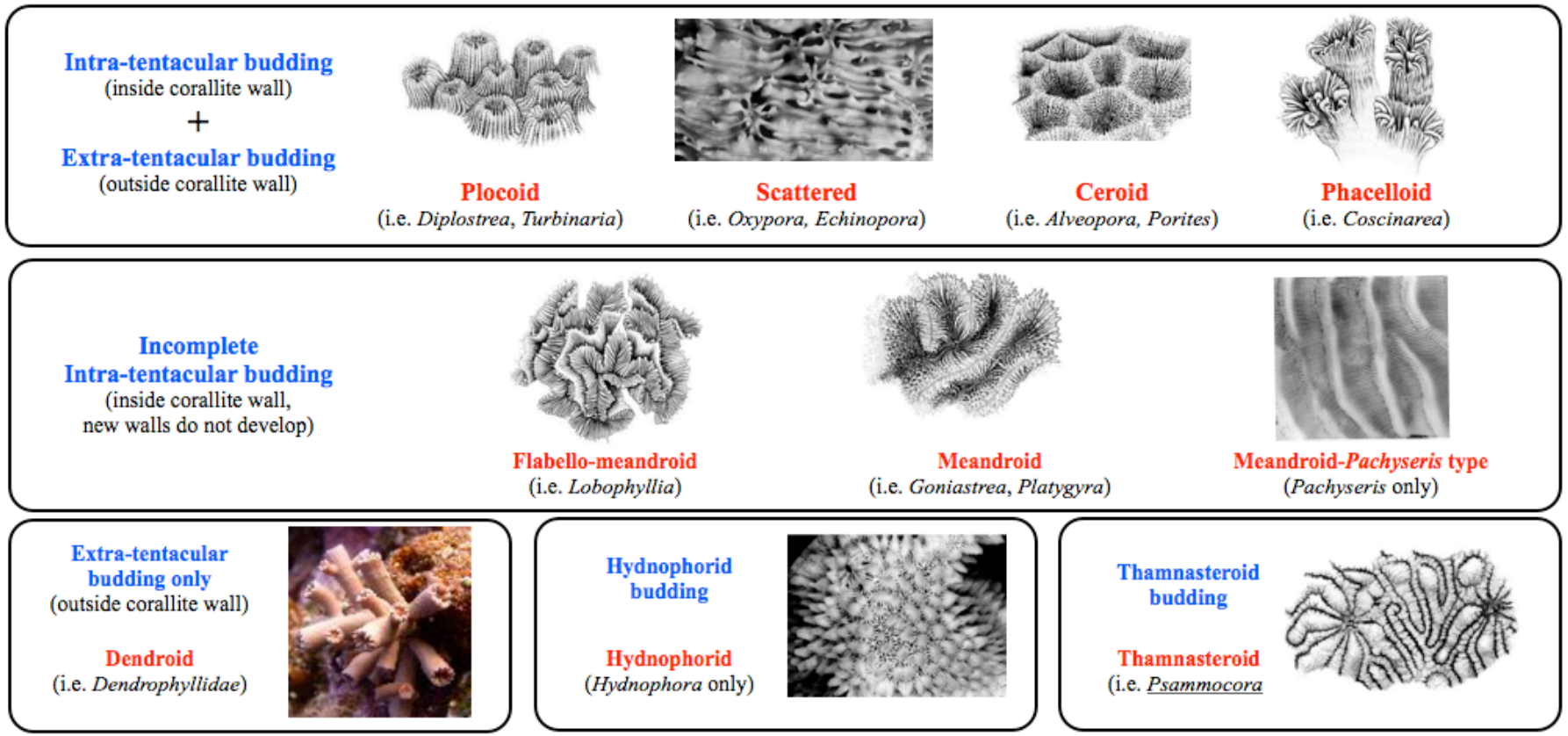


Figure 2.3 Budding types (red) possible for each corallite type (blue). Images and drawings from Coral ID (Veron, 2000).

Ceroid, plocoid, and all gradations between the two (sub-ceroid, sub-plocoid etc.) have been observed to undergo both intra- and extra-tentacular budding. Phacelloid corallites can also undergo both intra- and extra-tentacular budding. Dendroid corallite structures undergo extra-tentacular budding only. Corals with scattered corallite distribution and poorly defined wall structures (i.e. *Echinophyllia, Oxypora, Montipora, Echinopora*) have been observed to have both intra- and extra-tentacular budding. Meandroid, flabello-meandroid, and meandroid-*Pachyseris* type corallites predominantly divide via incomplete intra-tentacular budding.

Hydrophorid and thamnasteroid budding are special cases and the intra- extra-tentacular classifications become strained since it is difficult to determine where the wall structures actually are. Therefore, these budding types are referred to as thamnasteroid-budding and hydnophorid budding.

2.5.4. Aggression related physiological traits

2.5.4.1. Toxicity

Profiles of biologically active substances (allelochemicals) for 58 *Scleractinian* species are not consistent (Gunthorpe and Cameron, 1990a). Such inconsistencies between bioactivities have also been observed in soft corals (La Barre et al., 1986). Because bioactivity and thereby chemical defence is highly variable by colony, regardless of taxonomy, it should be considered idiosyncratic to individual colonies. The idea of typical chemical defence profiles for corals simply does not hold. In a related study (Gunthorpe and Cameron, 1990b) the bioactivity of toxins of nine corals in the families *Mussidae*, *Maviidae*, *Merulinidae*, and *Acroporidae* was temporally variable. Due to the lack of taxonomic and temporal consistency of bioactivity I suggest that toxicity not be included in trait-based analyses.

2.5.5. Thermo-sensitivity related physiological traits

2.5.5.1. Symbiont clade association

Symbiosis in corals is a functional term, not a taxonomic distinction. *Symbiodinium* vary in their cell morphology ultrastructure, circadian rhythms, growth rates, host infection ability, and photoacclimatization (LaJeunesse, 2001). Based on phylogenetics a total of eight *Symbiodinium* lineages or subgeneric 'clades' (A-H) and many clade subtypes have been identified. Defining *Symbiodinium* species in an ecologically meaningful way has been highlighted as a priority (for example Thornhill et al., 2008), but currently many taxa lack the phylogenetic or ecological support to justify their classification as a distinct species. This, and the ability of corals to partially switch clades as well as seasonal fluxuations in *Symbiodinium* density (Fagoonee et al., 1999), makes using *Symbiodinium* clades as a trait particularly difficult.

However, clade-level data is readily available (see online database GeoSymbios Franklin et al., 2011) and is ecologically relevant since it may influence both growth and thermal tolerance of corals (Little et al., 2004, Abrego et al., 2008, Jones and Berkelmans, 2010).

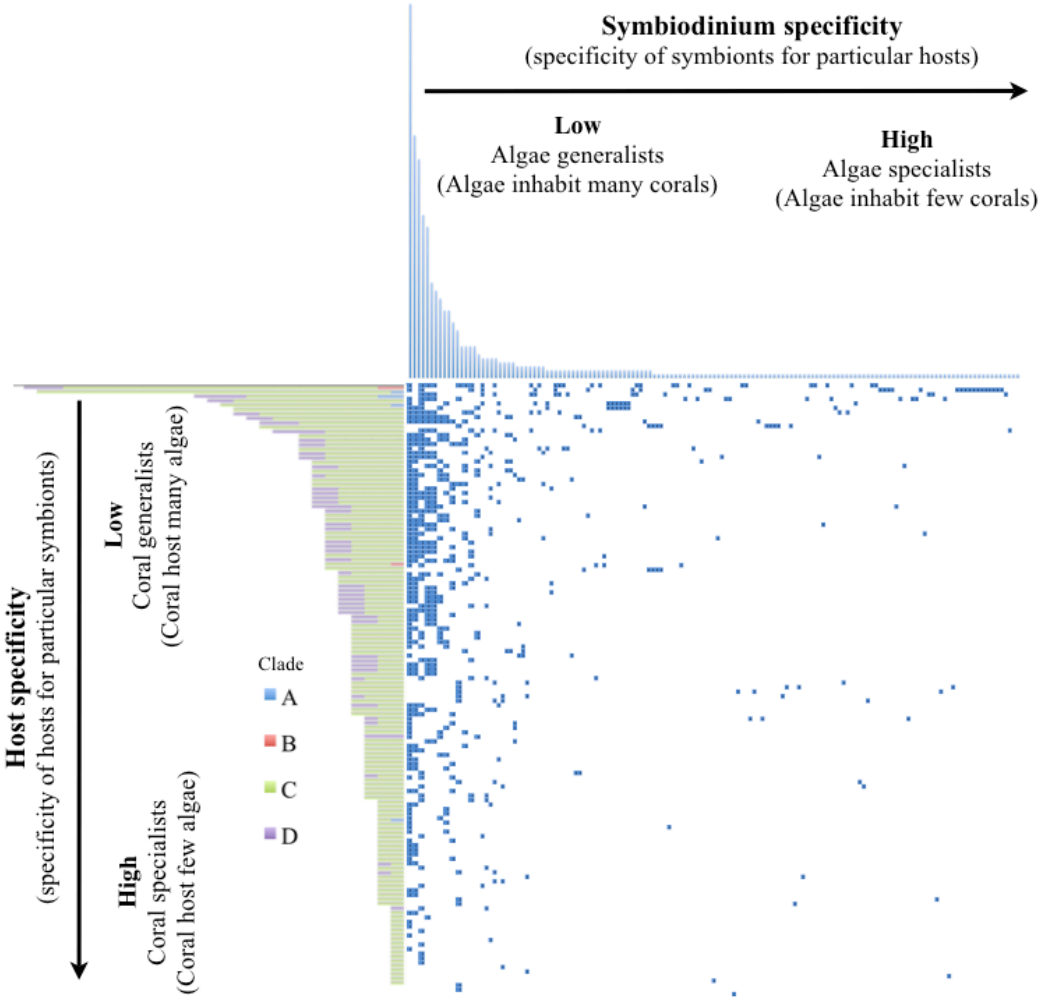
Corals associate most commonly with clade C but may also associate with clades A, B, D, F, and G. Some coral colonies contain only one type of *Symbiodinium* while others may contain multiple types. *Symbiodinium* are not equal in terms of their ability to confer properties such as thermo tolerance. Some members of clade D have been termed as disaster-taxa due to their notable thermo-tolerance (Correa and Baker, 2010). These disaster taxa become important during disaster events such as bleaching events since they can fill the ecological space created by the death of the competitors, thereby allowing the coral to persist. Clade C is thought to have a wide range of both temperature and salinity tolerance (McClanahan et al., 2003). Clade B has been shown to be specifically adapted to the cooler water temperatures and lower-light conditions of higher-latitude environments (Rodriguez-Lanetty et al., 2001). It has been suggested that the relationship between coral and Clade A is closer

to parasitism than mutualism and that this relationship may contribute to a reduced health state in Pacific corals (Stat et al., 2008).

Clade association is important for corals although perhaps equally important is the flexibility of such associations as switching partners may confer a functional advantage to the host coral (Cooper et al., 2011). For example, *Symbiodinium* type has been shown to vary by depth for some corals thereby allowing it to inhabit a greater depth range (Nir et al., 2011). The lack of partner switching along depth gradients in some species could be because their morphological plasticity allows them to compensate for lower light conditions thereby allowing the coral to maintain the same partner associations along wide ranging bathymetric gradients.

It is tempting to infer that some corals and *Symbiodinium* species are specialists (associating with only one partner) while others are generalists associating with may partners (see Figure 2.4). However, until *Symbiodinium* species are better defined one cannot discount that a coral species observed to host many *Symbiodinium* species might only be hosting one species with great genetic flexibility. If the phenomenon of specialists and generalist partners is real then this may well reflect coral life strategies and should be incorporated into trait-based studies. Another factor influencing the classification of 'specialist-generalist' labelling is that relationships that appear to be exclusive may simply be a result of under-sampling reflecting the fact that it is impossible to survey the hosts along all possible environmental gradients. Labelling corals as generalist of specialist can be done (see Figure 2.4) but must be interpreted with caution.

Figure 2.4 *Symbiodinium* clade versatility of corals present in Southwest Madagascar for which data is available. The x-axis shows how selective *Symbiodinium* algae are in terms of the coral host that they can inhabit (i.e. whether a *Sybiodinium* is a generalist which can inhabit many corals or a specialist that can only inhabit a few) with specificity increasing from left to right. The y-axis shows how selective coral species are in terms of the *Symbiodinium* algae they host (i.e. whether a coral is a generalist and hosts many different *Symbiodinium* or a specialist hosting only a few types of *Symbiodinium*) with specificity increasing from top to bottom. NB Whether or not the Symbiodinium shown are each separate species or whether some are genetic strains of the same species is under debate (see text) as *Symbiodinium* taxonomy is currently in flux.



2.5.5.2. Hardiness

Hardiness refers to how susceptible, resistant, and able to recover coral species are to bleaching, disease, and predation. It is likely that hardiness is due to a combination of several traits and as trait data accumulates, specific combinations of trait measurements can eventually replace 'hardiness' in trait-based studies. At present time however, it is reasonable to use observational data of hardiness as a trait. Such data is widely available and can be used with the caveat that it is really the result of many measurable physiological traits and should therefore be interpreted with caution.

While hardiness could have a range of trait attributes six are widely available (Carpenter et al., 2008): 'medium-high susceptibility to bleaching', 'medium-high susceptibility to disease', 'medium-high susceptibility to predation', 'medium-high resistance to bleaching', 'medium-high resistance to disease', and 'recovers quickly from bleaching or disease'. Observational data on hardiness is summarized in Digital Supplement 1.1.6 (adapted from Carpenter et al., 2008).

Some species are more likely to bleach than others under similar thermal regimes. In general, massive and encrusting species with thick tissues (i.e. *Goniastrea* spp.*, Platygyra* spp.*, Favia* spp.) tend to have greater bleaching resistance than branching corals with thin tissues i.e. *Acropora* spp.*,* branching *Porites* spp., *Stylophora* spp.*, and Seriatopora* spp. (Loya et al., 2001).

2.5.6. Immunology related traits.

Palmer et al. (2010) recently demonstrated how the relative investment in four key immunity parametres varies for different coral taxa. They found immunity parametres correlated strongly with both the disease and bleaching susceptibility of 15 *Scleractinian* corals from 12 families. The immunity parametres were: presence of melanin, size of melanin-containing granular cells, phenoloxidase activity, and fluorescent proteins. These four traits appear to be species specific and could be used in trait-based analyses once more data becomes available.

2.6. Phenological traits

2.6.1. Spawning schedule

Both the timing and frequency with which corals spawn and release larvae (in the case of brooders) is highly dependent on location. Therefore these traits can only be utilized if the spawning schedule for a particular region is well documented. Species-specific spawning schedules are available for many regions (see p. 180-184 Richmond, 1997) but not SW Madagascar.

2.7. Larval traits

2.7.1. Larval traits with sufficient data

The distance at which a larva settles from its parent is determined to large extent by environmental factors that interact with a suite of species-specific larval traits and this interaction ultimately determines the settlement success, dispersal distance, biogeographic patterns and abundance of *Scleractinian* corals.

Combining larvae survival times with distance to down-stream reefs and current speed allows for calculation of connectivity between reefs and highlights reefs that rely largely on self-seeding. Larval mortality is often due to starvation (Strathmann, 1985), predation (Thorson, 1950), physiological stress resulting from suboptimal environmental conditions (Pechenik, 1987), disease and genetic abnormalities (Rumrill, 1990). Estimating species-level differences in larval mortality rates in situ may well be impossible, although, parametres associated with larval survival potential can be estimated from laboratory cultures.

Coral larval biology has recently been reviewed (Gleason and Hofmann, 2011). While data is accumulating about the autecology of coral larvae, data paucity for most traits prevents integration into trait-based analysis with a few notable exceptions.

2.7.1.1. Larval association with symbionts

In the case of sexual reproduction, coral larvae can acquire symbionts through vertical transmission or by horizontal transmission (eg. Coffroth and Santos, 2005). Transmission mode is well documented (see Digital Supplement 1.1.5 adapted from Baird et al., 2009) with a number of important fitness implications.

Vertical transmission of symbionts occurs in all known brooding corals except the Isoporans, and in all spawning species examined to date for the genera *Montipora*, *Porites*, *Pocillopora,* and *Anacropora*, while horizontal transmission occurs in the remaining spawning corals. Thus generational shifts in symbiont populations present in the host can occur in spawning corals but tend not to occur in brooding corals (LaJeunesse, 2005). There are advantages and disadvantages with both vertical and horizontal transmission strategies. Vertical transmission guarantees that the offspring will establish successful association with *Symbiodinium* of the appropriate type. On the other hand, vertical transmission may prove metabolically expensive for the larvae to maintain thereby interfering with developmental processes, further, the environmental conditions in which the coral larvae settles may prove sub-optimal for the symbiont genotype (Douglas, 2008).

The advantage of acquiring *Symbiodinium* from the surrounding environment through horizontal transmission is that a higher *Symbiodinium* diversity within the coral host can be maintained, which increases the chance that *Symbiodinium* populations in the holobiont will be maintained even under adverse environmental conditions. The risk of horizontal transmission is that the coral host may fail to acquire *Symbiodinium* from the surrounding environment (Genkai-Kato and Yamamura, 1999).

2.7.1.2. Egg and larval size

Both egg and larval length or biomasses reflect the energetic investment that each species makes in each reproductive unit; it may represent a key difference in sexual reproductive strategy. This strategy difference may be sufficiently captured by the

trait reproductive mode. Generally, egg size is larger in brooding species than in spawning species. The relationship between egg/larva size and reproductive mode remains to be formally summarized using a broad dataset.

Egg/larval size has a number of survival implications beyond the well observed fact that large larva of brooding species are competent for settlement much faster than small larvae from spawning corals (Richmond, 1997). Egg size has been compiled for at least ten Caribbean species (Szmant, 1986) and nearly 50 observations have been compiled for Indo-Pacific (Fadlallah, 1983). Since these studies more egg and larval size data have become available but remain to be compiled. The utility of egg and larval size as a trait will depend on the quantity of trait data available for the species in a particular area.

2.7.1.3. Egg colour

Egg colour reflects pigmentation and possibly the eggs ability to protect itself against harmful radiation. Egg colour is easily observed and has been well documented for corals on the GBR with Babcock et al. (1986) providing a summary of egg colour for nearly 100 species. Therefore egg colour can reasonably be included as a trait for many Indopacific locations with current levels of data availability.

2.7.1.4. Larval motility

Larvae may swim or crawl epibenthically. Larvae from spawned corals swim (I could find no records of spawned larvae that crawl) while larvae from brooded corals have been observed to swim or crawl (Fadlallah and Pearse, 1982, Fadlallah, 1983, Paz-Garcia et al., 2007). The motility mode has implication for dispersal distance. The last large-scale summary of larval motility was nearly three decades ago (Fadlallah, 1983).

2.7.2. Larval traits with data paucity

Three important larval traits with data paucity are larval metabolic constraints, competency period, and position in the water column over time. Between these three

trait categories I could only find species-level data for 26 species. Here I briefly discuss the importance of each of these traits:

- Based on laboratory cultures, there appears to be species-level differences in both the median and maximum larval lifetime, in other words, different coral species larvae starve at different rates. Graham et al. (2008) observed large differences in both the 50 percent mortality and maximum survival time for five coral species (all broadcasters) and suggested that larval mortality curves based on metabolic constraints is a potentially important trait.

- Larval competency period is not the same as maximum survival times as larvae lose their ability to recruit often well before death from starvation. The ratio between maximum survival and maximum competence has been calculated for soft corals (Ben-David-Zaslow and Benayahu, 1998) but not for *Scleractinian* corals. The time required after spawning or larval release to become competent varies greatly between species with brooding corals often having competent larvae within hours while for spawning corals it often takes days. Likewise the total amount of time larvae can remain in the competent stage varies between coral species.

- Tay et al. (2011) observed a downward shift in the vertical position of three coral species larvae in the water column. They noted that the sinking rate was inconsistent with peak settlement competency periods and suggested that such inconsistencies could have serious implication for the success of settlement in different coral species. A temporal inter-play between competency timing mortality rates and vertical movement are all-important in determining distribution. Therefore these three traits require further investigation.

2.8. Conclusion

A comprehensive schema of coral life-history traits has been presented under the five categories: 1) morphological, 2) behavioural, 3) physiological, 4) phenological and 5) larval traits. Data availability varies greatly, as do units of measurement, and environmental plasticity of the traits.

Based on both suitability and availability for the species in Southwest Madagascar, 26 traits were selected to be included in this study; these traits are summarized in Table 2.7.

Table 2.7 Summary of traits selected for use in this study

Trait Level 1	Trait level 2	Traits
Morphology	Colony level	Colony formation
		Colony morphology
		Maximum Surface index
		Minimum Surface index
		Morphological plasticity
		Attachment to reef
		Colony growth strategy
		Maximum colony size
	Corallite level	Corallite form
		Corallite spacing
		Corallite size
	Soft tissue level	Tentacle length
		Polyp dimorphism
		Polyp colour
Behaviour	Feeding related	Diel tissue expansion pattern
		Daytime tissue projection
	Sediment shedding	Active sediment shedding behaviour group
Physiological	Sexual reproduction	Sexuality
		Larval development
		Spawning behaviour
	Asexual reproduction	Asexual reproductive mode
	Growth related	Intra-colony budding pattern
	Environmental sensitivity	Symbiont clade association
		Hardiness
Larval biology		Larval association with symbionts
		Egg colour

3.
Description of study regions

Declaration: *The only data in this chapter collected by the author (jointly with Sophie Benbow, Blue Ventures) was clod card data for three reef sites, which was added to an existing clod card data set for four reefs. Data presented on coastal bathymetry, large-scale currents, winds, cyclones, tides, sedimentation, and water temperature was compiled using reference texts, and satellite imagery data from NOAA and Blue Ventures.*

3.1. Introduction

The overarching aim of this thesis, to test whether supplementing species data with life-history trait data can provide useful information beyond than gleaned from species composition alone, was achieved using data collected in Southwest Madagascar between October 2009 and February 2010.

Madagascar is the fourth largest island in the world extending from 10 to 25° South with a coastline approximately 4,500 km in length. It has a surface area of 590,000 km^2, which is roughly the size of France. Scattered around the island are approximately 270 small continental islets (Cooke et al., 2000). Madagascar supports some of the most biodiverse coral reefs in the Southwest Indian Ocean with an estimated 6,000 recorded reef-associated species, including 752 fish species and 340 coral species (McKenna and Allen, 2006).

Three study regions along the Southwest coast of Madagascar were surveyed: Tulear in the south (23°23´S-43°42´E), Velondriake further north (22°04´S-43°14´E), and Ranobe (23°03´S-43°35´E), which is located between the two (Figure 3.1). These were selected because of their location along: 1) a fishing intensity gradient and 2) a sedimentation gradient which both increase southward. The fishing gradient is due to a northward migration of fishermen as exploited fisheries in the south collapse, while the sediment gradient is due to inland and mangrove deforestation and the position of the three major rivers in the Southwest: the Onilahy, the Mangoky, and the

Fiherenana (Figure 3.1). These gradients offer the opportunity to examine how species composition and trait-combination composition on reefs vary along them.

In this chapter the geographic features of each study region and the location of surveyed reef sites in each region are presented. The major environmental factors characterizing Southwest Madagascar are then discussed, highlighting differences between the three study regions. The major reef typologies found in the three study regions are then introduced followed by a brief discussion of the human populations in Southwest Madagascar and their relationship to local reefs. .

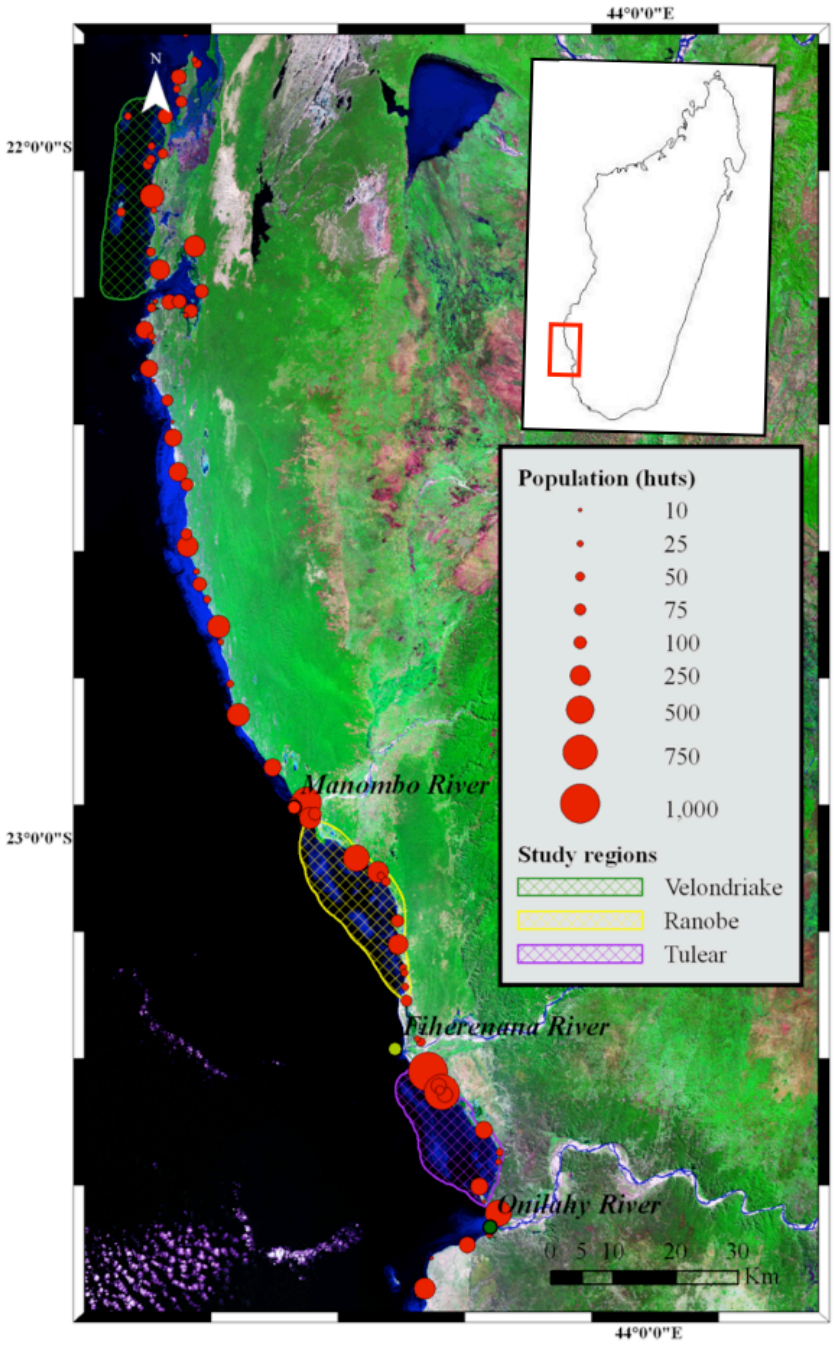


Figure 3.1 Map of the three study regions: Velondriake (green boundary line), Ranobe (yellow), and Tulear (purple). Fishing intensity increases southward as reflected by the number of fishing huts in each region, counted from satellite images (red circles). The position of the three major rivers (from north to south: Manombo, Fiherenana, and Ouilahy river) in combination with inland deforestation results in a sedimentation gradient increasing southward.

3.2. Study regions and reef sites

In total, 68 reef sites in three study regions were surveyed along nearly 200 km of coastline. Two of these sites were later dropped due to photo quality (R18) and lack of any coral (T1) resulting in a total of 66 reef sites. Reefs in the region are poorly mapped and therefore satellite images were used to locate shallow reefs. I used satellite images of the region to facilitate talks with fishermen, dive operators (Mada Blue Dive Centre, Le Grand Bleu, and Atimoo Plongee), a number of non-governmental organizations (Blue Ventures, Reef-doctor, WWF, and the Southwest Regional Environmental Athority or SAGE), the Madagascar Fisheries Department in Tulear and graduate students at the Institut Halieutiqu et des Sciences Marines (IHSM). Based on these conversations and satellite imagery I identified reef locations and selected the sites to survey.

The surveyed reefs differed in physical structure but were classified into six major reef types (discussed in section 3.4). For simplicity they were also categorized to one of three geomorphological classes: fringing reefs, patch reefs, and spur and groove systems. This classification is coarse, as some reefs did not fit neatly into these classes; nonetheless this scheme permits a rough overview of the types of reefs present in each of the three study regions (Table 3.1)

Table 3.1 Summary of study sites by study region and geomorphological structure.

		Geomorphology			
Region	**Coastline**	**Fringing**	**Patch**	**Spur and groove**	**Total**
Velondriake	45 km	6	19	5	30
Ranobe	35 km	0	15	8	23
Tulear	25 km	4	6	3	13
Total	105 km	10	40	16	66

Sampling effort in each region was proportionate to its coastal length. While every attempt was made to create a balanced sampling design, there were inherent differences between the regions in terms of the quantity of reef types present. For example, there were no fringing reefs in the Ranobe study region.

3.2.1. Andavadoaka (Velondriake)

The northern most study region is called 'Velondriake' which means 'to live with the sea' in the local Malagasy dialect of Vezo and is also the name for the fishing association that has been set up between 21 neighbouring villages here. The fishing association is a joint collaboration between Blue Ventures Conservation (BV), IHSM, Wildlife Conservation Society (WCS), and local fishing communities. The intent of this collaboration is to develop a network of no-take zones in the Velondriake region, which spans just over 800 km^2. This network is currently benefiting over 10,000 people (Harris, 2007).

Census data collected in Andavadoaka, one of the largest fishing villages in Velondriake, revealed that 71 percent of its population relies on fisheries for their main source of income (Langley, 2006). This is typical for the Velondriake study region. Due to the remoteness of the Velondriake study region a limited amount of tourist frequent the area.

Velondriake stretches from 15 km south of the village of Morombe in the north to 15 km south of the village of Andavadoaka. An uneven coastline and widely spaced barrier islands characterize the region. Reefs near the village of Andavadoaka have been well surveyed and monitored by Blue Ventures while reefs further away are less well characterized. A total of 30 reef sites were sampled in this study region (Figure 3.2).

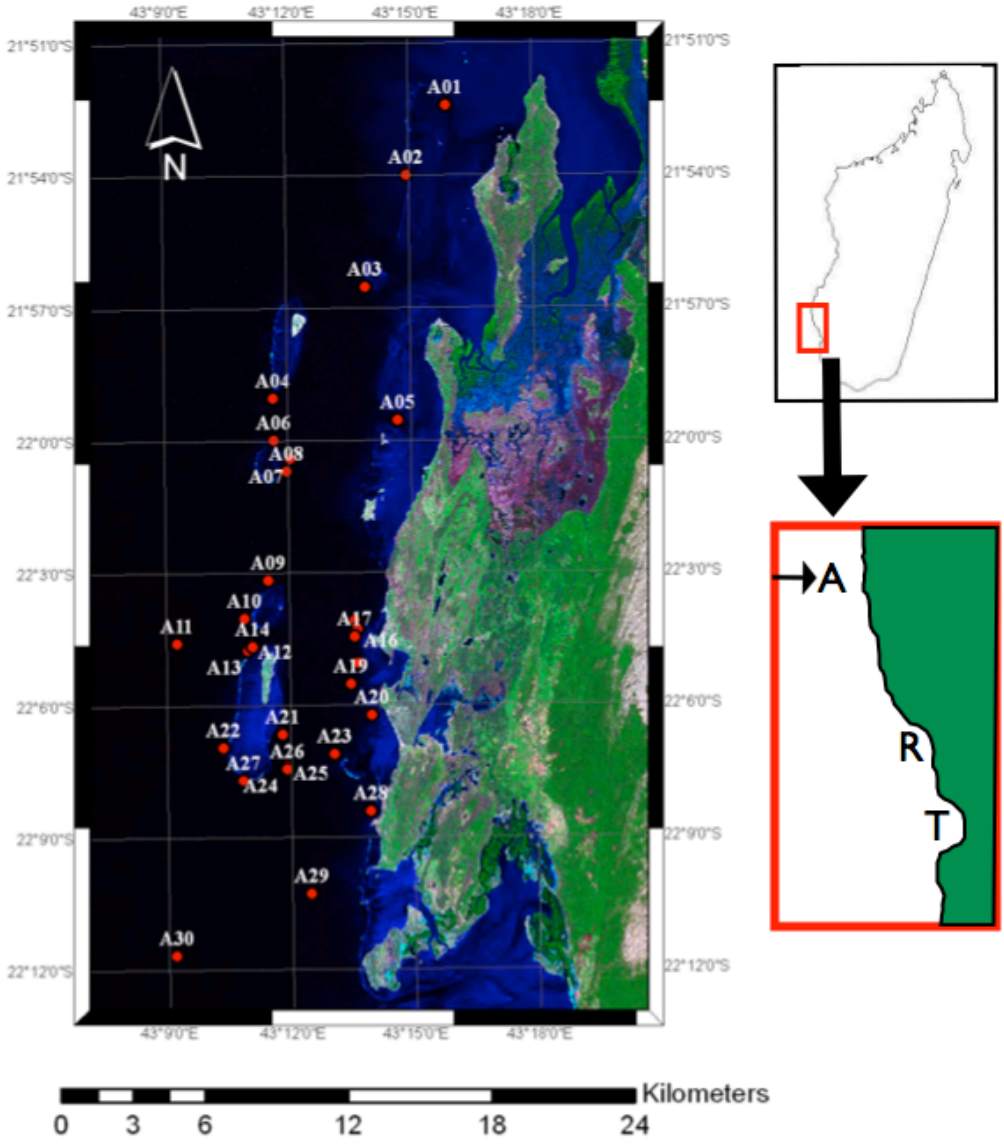


Figure 3.2 Satellite map of the Velondriake study region with the 30 reef sites surveyed highlighted in white (A01-A30).

3.2.2. Ranobe

The bay of Ranobe is sheltered by a barrier reef that stretches along the 35 km long coastline. Within the bay mangroves can be found to the north and south while sea grass beds and shallow patch reefs are scattered throughout. In this study region, the mangroves have been heavily deforested, the seagrass bed damaged by beach seines and the patch reefs severely damaged by bleaching and destructive fishing practices. The bay is shallow and rarely exceeds a depth of eight metres within the lagoon. During the rainy season the bay experiences high levels of sedimentation from river mouths immediately to the north and south. Due to the extensive damage to the mangrove systems at the river mouths sediment filtration is limited. While there is a moderate tourist industry in Ranobe, the main livelihood for the Vezo remains fisheries.

Two reef types dominate the lagoon: large, shallow patch reefs and smaller, deeper patch reefs. The large shallow patch reefs have diametres ranging from 0.2 to 1.4 km and have been heavily damaged by destructive net fishing techniques including the use of 1.5 km long fine meshed beach seines or 'Tarikaky'. The only place where live coral can be found today on the larger patch reefs is on the seaward facing edge. The shallow plateaus of these patch reefs are only 1-1.5 m deep and are all covered with *Acropora* spp. rubble and a thick carpet of macro algae with *Turbinaria* sp. being dominant. Outside the barrier, and in the passes where the current is strong and where fishing is difficult, observed coral cover is higher. A total of 24 reef sites were surveyed in the Ranobe study region (R18 was later dropped due to issues with photo quality; Figure 3.3).

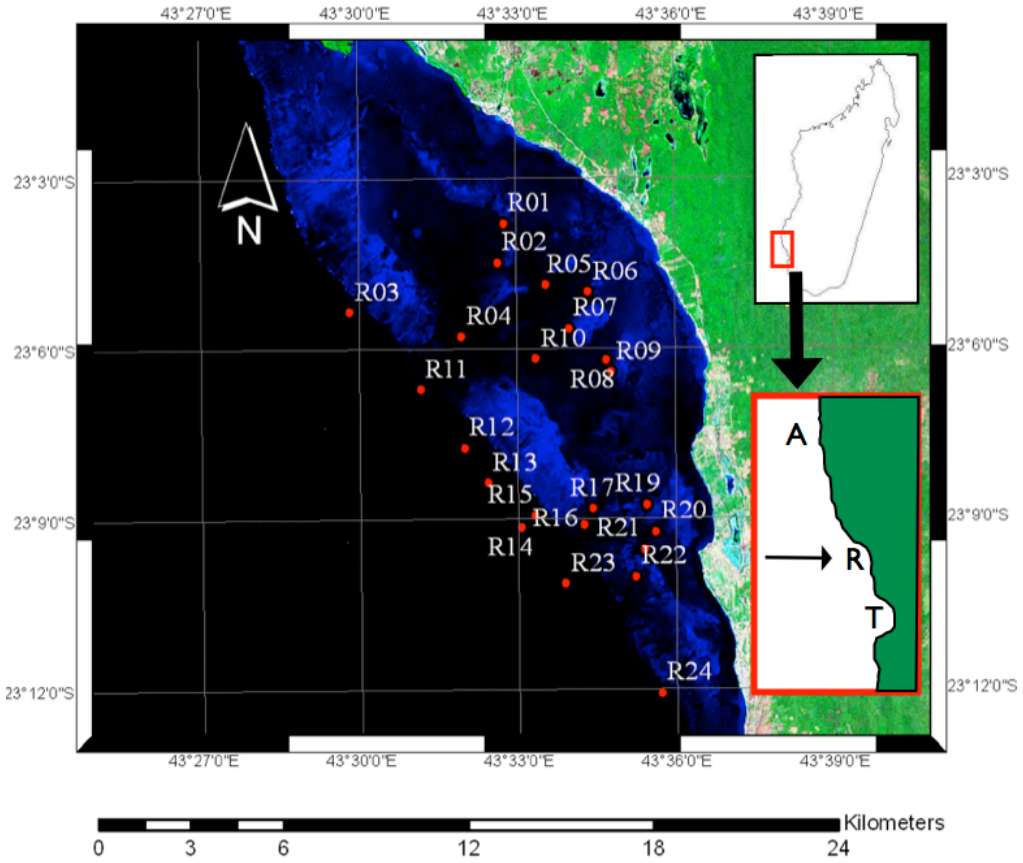


Figure 3.3 Satellite map of the Ranobe study region with the 24 reef sites surveyed highlighted in white (R1-R24). R18 was dropped due to poor photo quality and is therefore not shown.

3.2.3. Tulear

The Tulear study region is the smallest of the three surveyed with only 25 km of coastline. However, it has the highest population density; Tulear is the largest city in the south of Madagascar. The most recent high-resolution census data states that Tulear had a population of 101,661 in 2001 (*Ilo* Project, a joint project between Cornell University and PACT accessible at www.ilo.cornell.edu/ilo/data.html). The projected increase in Tulear's population between 1993 and 2008 was 53 percent and has been predicted to increase an additional 49 percent between 2008 and 2022 (www.instat.mg). The rapidly growing population is increasing the pressure on an already stressed reef system through both overfishing and the disposal of human waste on the beaches where the tides are used to flush it away (personal observation; Harris et al., 2010)

The reefs of Tulear were at one time the most well studied in Madagascar. From 1961-1970 intensive research efforts were undertaken out of Tulear's Marine Station resulting in approximately 400 scientific reports and Pichon's 490 page volume of *Atoll Research Bulletin* (1978). With the exception of a 35-page section in the *Atoll Research Bulletin* the reports are all in French and most remain as reports in places not easily available making their accessibility limited. While research was conducted in the following decades, those resulting reports and findings are also not easily accessible.

The most prominent feature of the study region is the 19 km long Grand Récif whose reef flat area is approximately 33 km^2 with the back-reef slope lying 1.8 – 8.5 km off shore. On its seaward side, a well-formed spur and groove system is present. On the landward side is a relatively shallow lagoon with depths of around ten metres throughout, with the exception of the north and south passes where depths reach 17 metres.

A total of 13 sites were surveyed in the Tulear study region, however, one of the sites (T01) was later dropped as no living coral could be found and coverage consisted entirely of coral rubble and macroalgae.

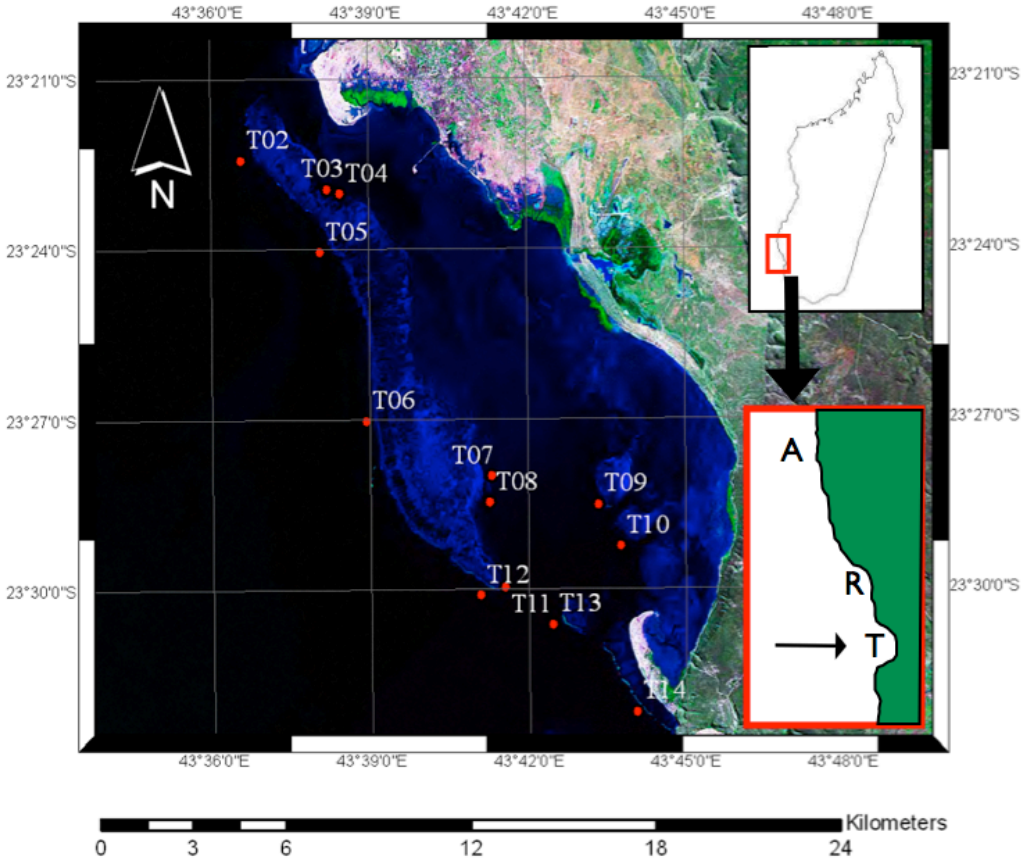


Figure 3.4 Satellite map of the Tulear study region with the 13 reef sites surveyed highlighted in white (T1-T13). T1 was entirely covered with algae and no coral could be found and is therefore not shown.

3.3. Major Regional Environmental Factors

3.3.1. Bathymetry

Madagascar's continental shelf has an area of around 117,000 km^2 (Figure 3.5) with a width that varies from over 100 kilometres to only a few kilometres (Ranaivoson, 1996). Near Tulear it is uniquely narrow due to geological faulting; in places the 200 metres isobaths are located only three to four nautical miles offshore (Figure 3.6). Because of the narrow continental shelf and access to deeper waters, local Vezo fishermen have been known to catch specimens of the 'living fossil' *Latimera chalumnae* (Coelocanth) in 'Jarifas', deeply cast, rope nets intended for sharks (Heemstra et al., 1996).

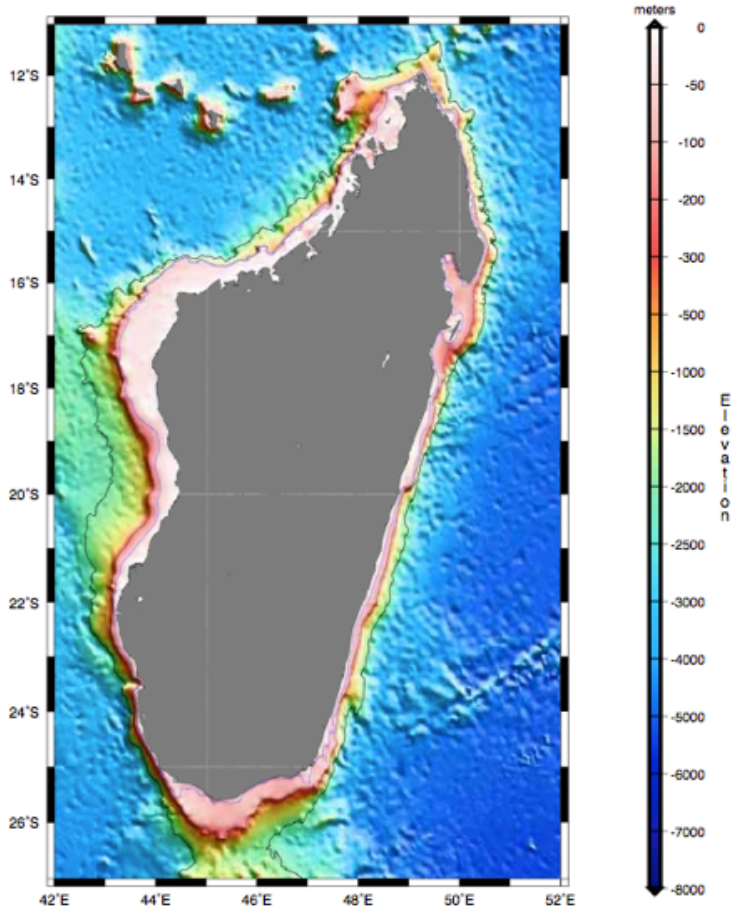


Figure 3.5 Bathymetric map of Madagascar. Note the narrow continental shelf in the Southwest where the study regions were located (map from Naqvi, 2010).

The continental shelf is also relatively narrow in Ranobe and Velondriake. The large-scale bathymetry is similar for the three study regions with comparable spacing of 500 metre contour lines down to about 2000 metres (Figure 3.6).

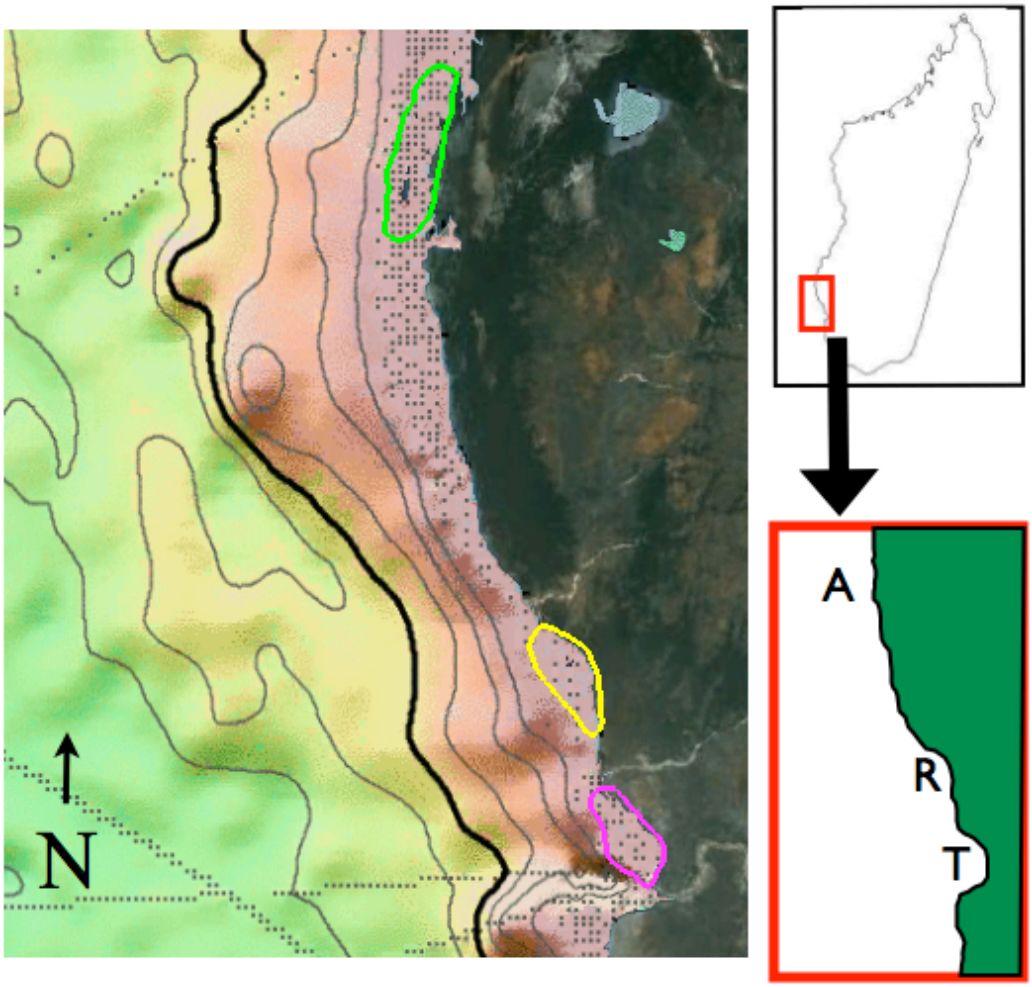


Figure 3.6 Bathymetry in the location of the three study regions: Velondriake (green), Ranobe (yellow) and Tulear (purple). The colours and 500 metre contours represent variations in seafloor depth. Points on the map show the location of deeper water soundings. The map was created using a global dataset which includes 290 million depth soundings compiled by investigators at SIO, NOAA, NGA, U.S. Navy, and GEBCO (Becker et al., 2009).

While large-scale bathymetry is similar between regions, smaller scale detail varies between sites. Detailed spectral bathymetry maps are available for the Velondriake and Ranobe study regions (Roy et al., 2009). These maps are in accordance with the depths observed at each surveyed reef site inside or around the barrier reefs. Although the depths of these spectral images underestimate the depths outside the barriers, the maps are a useful overview of the bathymetry in the area.

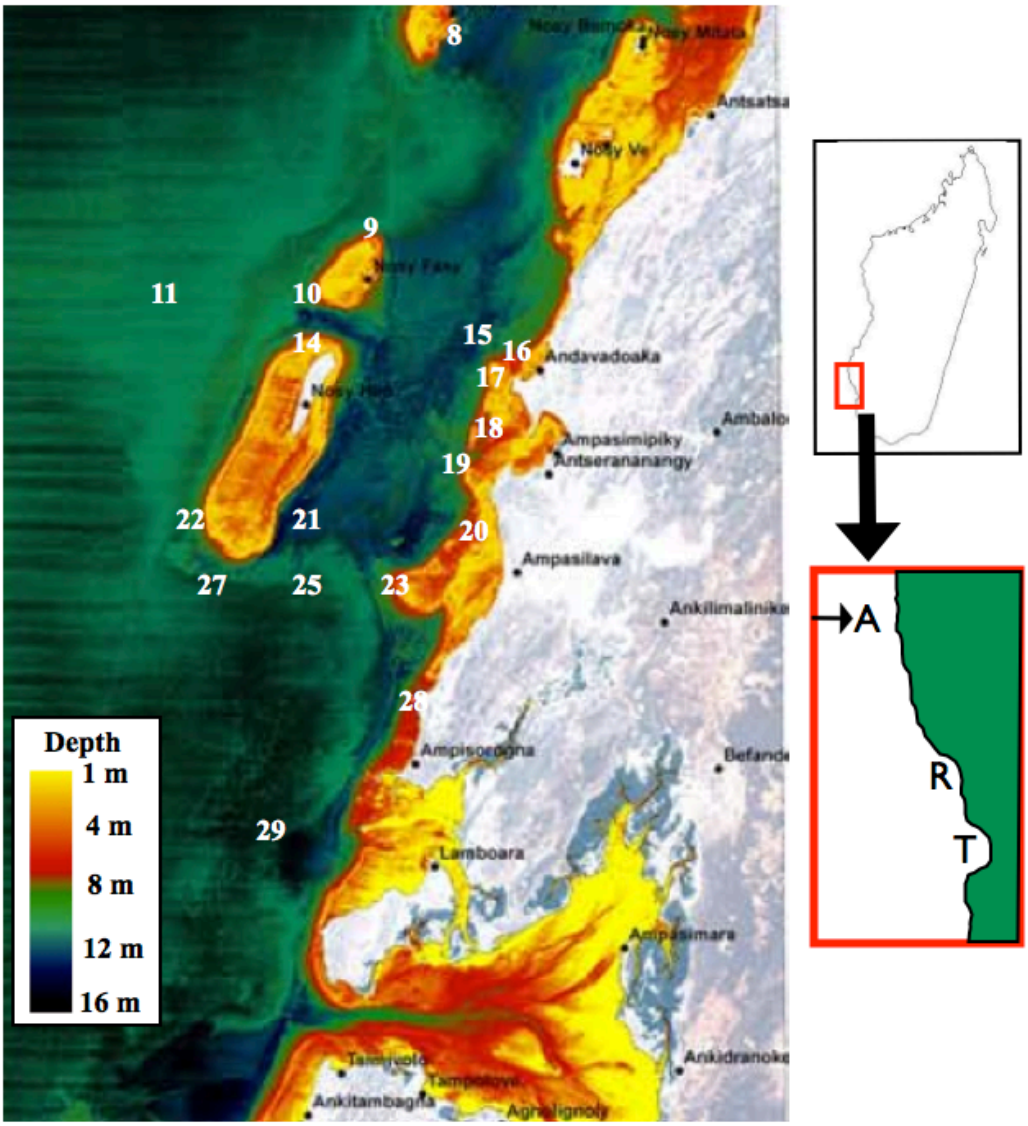


Figure 3.7 Spectral bathymetry data for Velondriake (adapted from Roy et al., 2009) with reef sites surveyed numbered in white. Spectral bathymetry maps were not available for the region north of Andavadoaka and therefore some survey sites are not visible on the map.

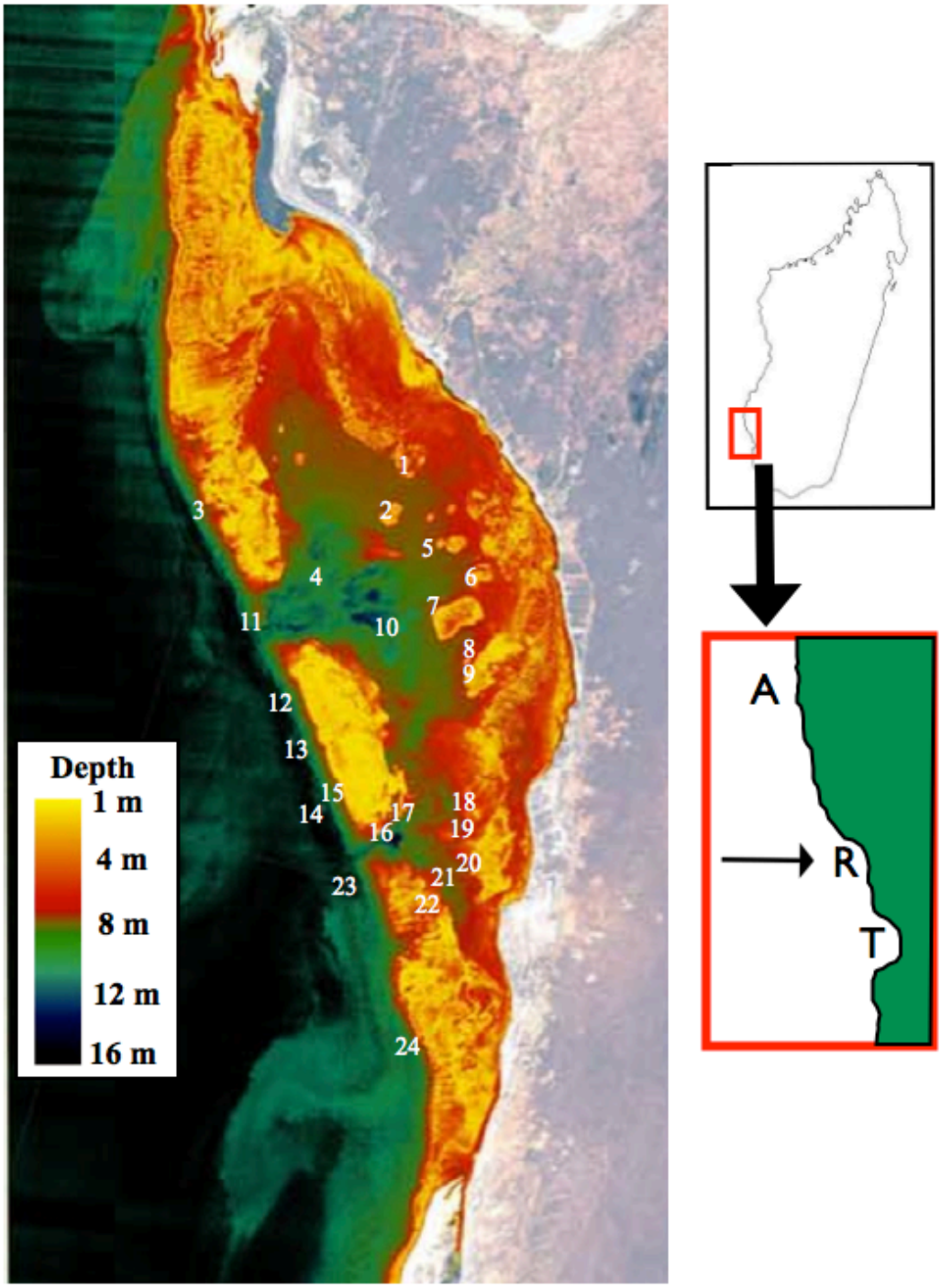


Figure 3.8 Spectral bathymetry map of Ranobe (adapted from Roy et al., 2009) with reef sites surveyed numbered in white. Note the shallow lagoon and steep drop-off outside the barrier.

A spectral bathymetry map was not available for Tulear. The bathymetry for Tulear is similar to that of Ranobe with a shallow lagoon, generally not exceeding ten

metres in depth. Outside the barrier the bottom gently slopes down to about 50 metres after which the drop-off becomes steeper.

3.3.2. Large scale currents

The main water bodies influencing the region are the oligotrophic South Equatorial Current (SEC), the Madagascar Current which brings up nutrient-rich waters from the south, and a gyre system in the northern Mozambique channel (Cooke et al., 2000). Where the SEC meets the East Coast of Madagascar at 16 - 18° S it splits into two major branches: a northbound branch (average velocity 0.58 m s^{-1}, average depth 258 metres) and a southbound branch (average velocity 0.33 m s-1, average depth 166 metres; Schott et al., 1988). Peak SEC flow occurs in July-August while the minimum flow is February-March.

When the southbound branch on the East coast of Madagascar reaches the southernmost tip of the island it splits into a northbound and westbound branch. The northbound branch of the Madagascar current continues north along the east coast to Il Juan de Nova (17.31S, 43.56E) where it feeds into a semi-permanent anticlockwise gyre in the north of the Mozambique channel and a less well-defined anticlockwise gyre in the south of the Mozambique channel (Figure 3.9). The northbound current also results in a quasi-stationary clockwise eddy to the south of Il Juan de Nova (Saetre and Silva, 1984). On the northeast coast of Madagascar, the northward branch of the SEC rounds the northern tip of the island before feeding into the gyre system in the northern Mozambique Channel.

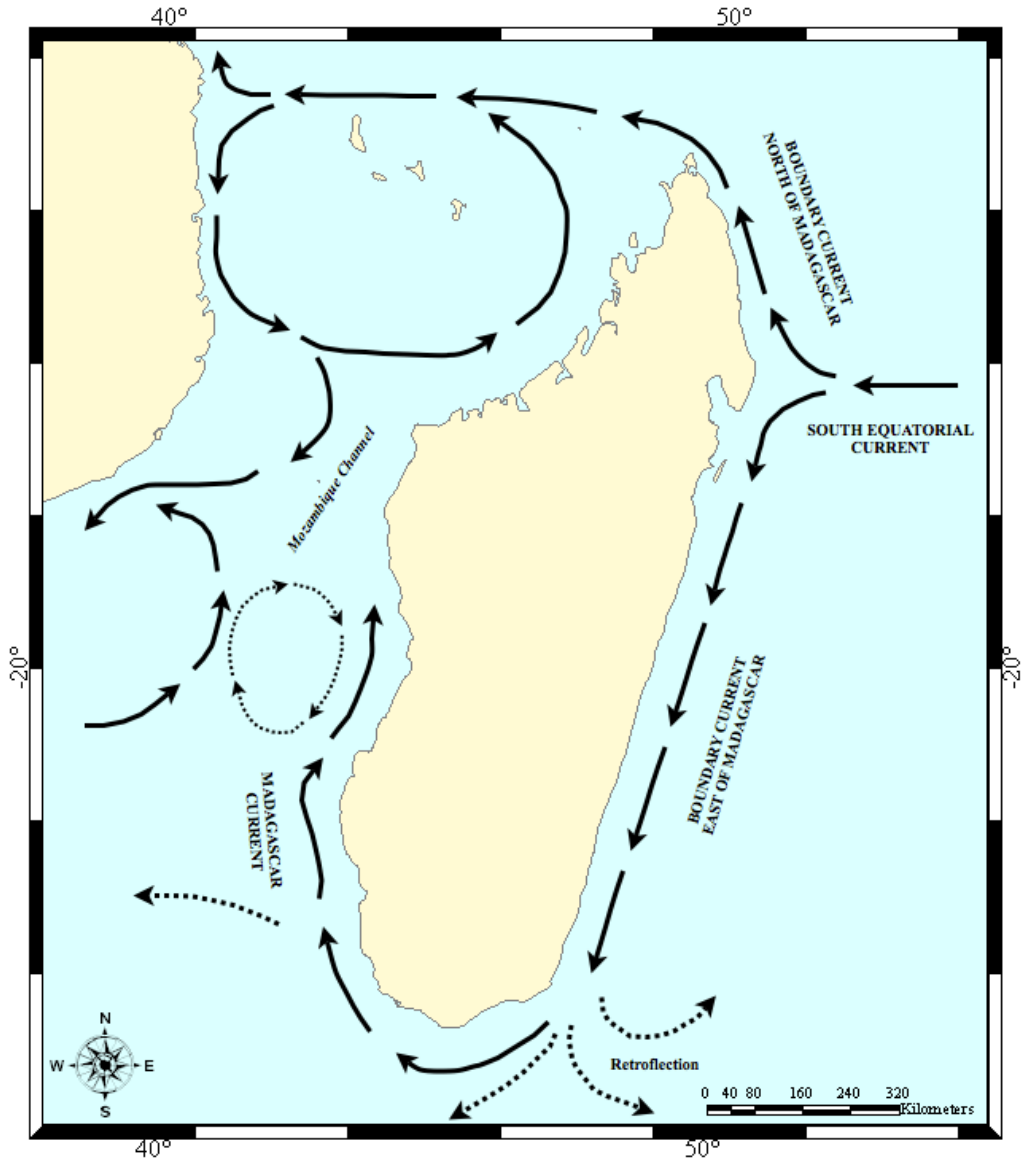


Figure 3.9 Major currents around Madagascar. Map redrawn from Cooke et al., (2000).

3.3.3. Local currents

The three study regions are all heavily influenced by the northbound branch of the Madagascar current (Figure 3.9). It is important to note that the smaller-scale inshore currents over the continental shelf may result in complex local patterns for each study region. While mapping small-scale currents was not possible for all 66 reef sites in this study, it is reasonable to make generalized observations about the

influence of currents at reef sites based on site position in relation to breakwater, local bathymetry, and direction of the major northward Madagascar Current.

3.3.3.1. Methods: collection of clod-card data

For one study region, Velondriake, the general influence of the currents was explored in more detail. Clod card data was collected for 3 reef sites in collaboration with S. Benbow (Blue Ventures) in October 2009. Similar data had been collected by Blue Ventures in 2008 for a further four sites. Clod cards are used to measure the relative strength of currents near the reef surface by calculating the dissolution rate of a material fixed to the reef surface. Clod cards were constructed by fixing a cylindrical section of *Plaster of Paris* (the clod) onto a plastic backing (the card). Before fixing the clod to the card, the clod was carefully weighed. On the reef, clod cards were fixed onto metal stakes and flagged so that they could easily be located upon retrieval the following day (Plate 3.1). Three clod cards were evenly spaced along each reef. The clod cards were kept in plastic Ziploc bags until immediately before fastening them onto the metal stakes. This allowed for recording an exact start time for the dissolution of the material. The clod cards remained on the reef for a 24-hour period after which they were collected, allowed to dry thoroughly, and then weighed. The dissolution rate was calculated as:

$$Dissolution\ rate\ (g\ day^{-1}) = \frac{clod\ weight\ before\ (g) - clod\ weight\ after\ (g)}{Total\ time\ on\ the\ reef\ (days)}$$

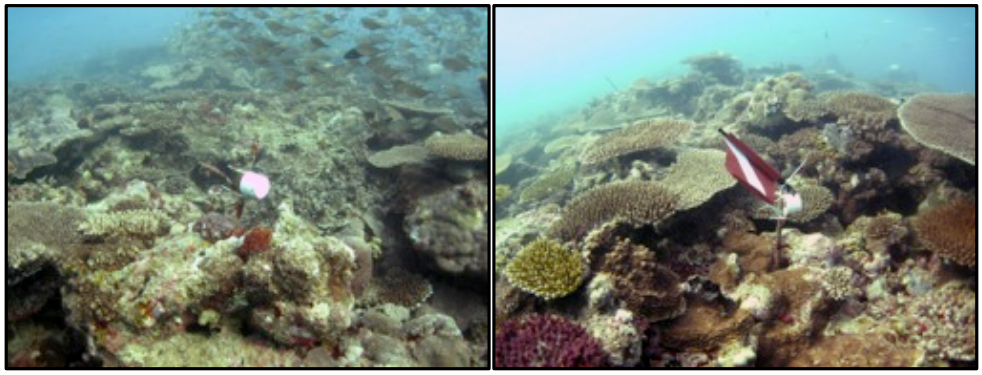


Plate 3.1 Images of deployed clod cards at site A25. Plaster of Paris clods (white) were fixed onto small plastic cards that were then fixed to a metal post and flagged.

3.3.3.2. Results: clod-card data

As expected, the current strength slows in the shadows of barriers facing south i.e. north of the largest island, Nosy Hao (dissolution rate of 26.5±4.5 g day^{-1}), and in the slightly deeper lagoon in the shadow of reefs to the south (dissolution rate of 29.8±1.5 g day^{-1}). While these short-term current measurements are merely snapshots of the current they are still useful in demonstrating the 'shadow effect' of slowed currents behind southward facing barriers. In addition, the deepest site (35 metres; NB the spectral bathymetric map is misleadingly shallow for this site) experienced a slower current (37.4±1.8 g day^{-1} dissolution rate) than shallower sites with similar direct current exposures (three most southern sites; Figure 3.10).

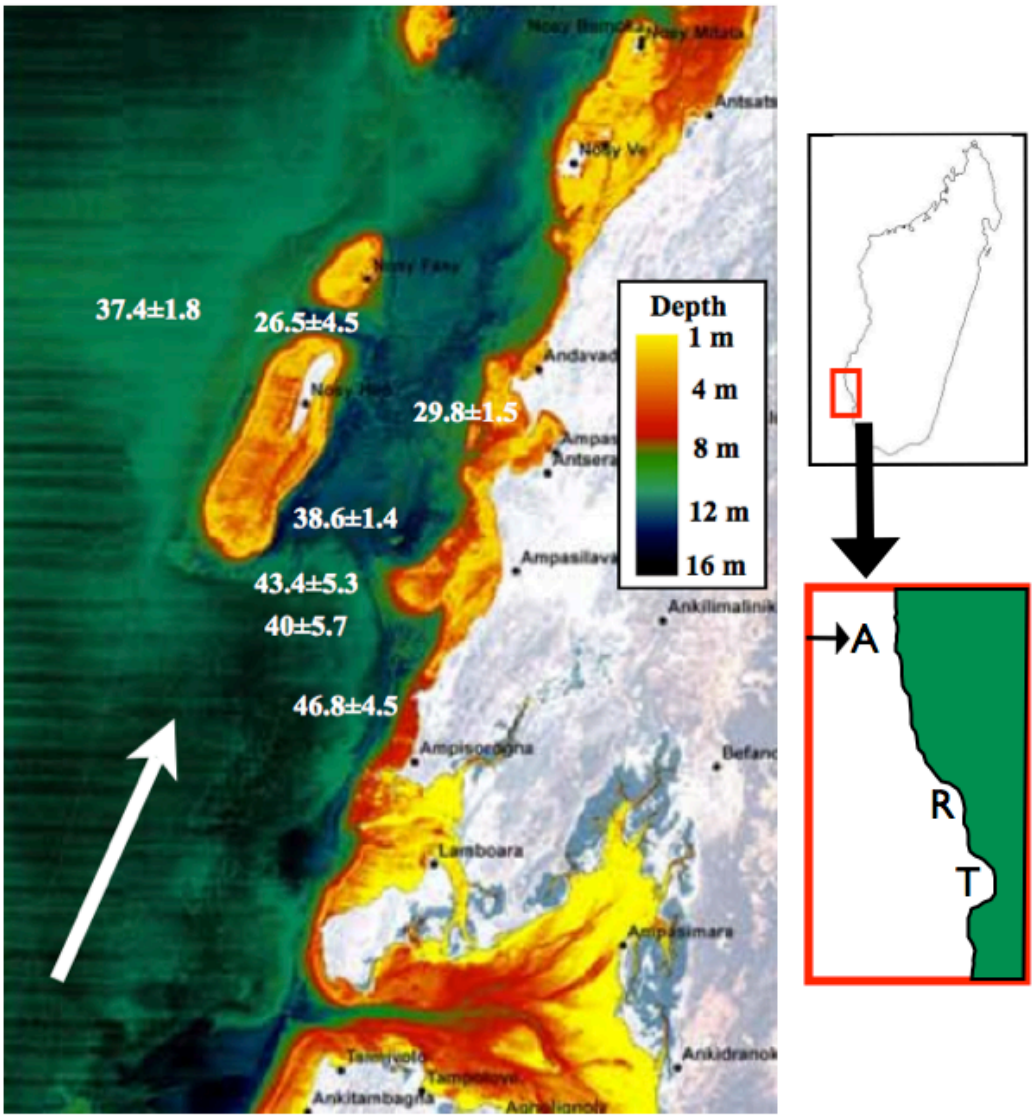


Figure 3.10 Current strength at seven reef sites in the Velondriake study region. The current strength is given in dissolution rates (g day^{-1}) of clod cards and the standard deviation of the three clod card samples per reef is indicated. The white arrow shows the major current direction. The colour indicates depth as predicted by spectral bathymetry. Note the decreased current speed behind southward facing barriers.

3.3.4. Winds and Cyclones

The two main wind systems influencing Madagascar are the Southeast Trade winds and the monsoon. The Northeast monsoon occurs from November to March while the Southeast monsoon occurs from April to October; both monsoons have an average wind speed of 3.5 m s^{-1}. The Southeast Trade winds blow strongest between August and April with a median wind speed of 6.1 m s^{-1}. The boundary position

between these two systems is determined by a zone of high pressure over the Mascarenes and a zone of low pressure over the Mozambique channel (Cooke et al., 2000).

Cyclones occur frequently during the warm season, which lasts from December to March. Cyclone paths normally start northeast of Madagascar and then move Southwest, curving around the northern tip of the island and into the Mozambique Channel. The cyclones then follow the coast down to about Morondava (S 20.16, E 44.14) before heading southeastward into the channel where they usually blow out. Sometimes, however, the cyclones follow the coastline further south than Morondava to the Southwest of Madagascar and impact the northern-most study region (Velondriake).

3.3.5. Tides

Tides influence access to reefs by the local fishing people. At low tides reefs are easier to locate, glean, and fish using a drag net. The tides are also important for the morphological development of reefs. The tides in the study regions are relatively high with a mean spring tidal range between three to four metres. Tidal ranges in the three study regions are similar.

3.3.6. Nutrients and Sedimentation

Along the East coast of Madagascar, nutrient and sediment levels are generally low as the SEC is an oligotrophic current. Along the West coast of Madagascar both nutrient and sediment levels are significantly higher since all major rivers drain along it. In addition West Coast currents are rich in nutrients pushing in from the South and also because of greater mixing with bottom water within the Mozambique Chanel (Cooke et al., 2000).

Real-time imaging of chlorophyll *a* densities is available from NASA's Goddard Space Flight Center (GSFC) MODIS Aqua satellite. While such images provide just a snapshot, they can still be useful in illustrating the importance of river mouth

position to nutrient and sediment distribution in the study regions. As can be seen in Figure 3.11 both Tulear and Ranobe experience higher nutrient and sedimentation levels than Velondriake due to river mouth position.

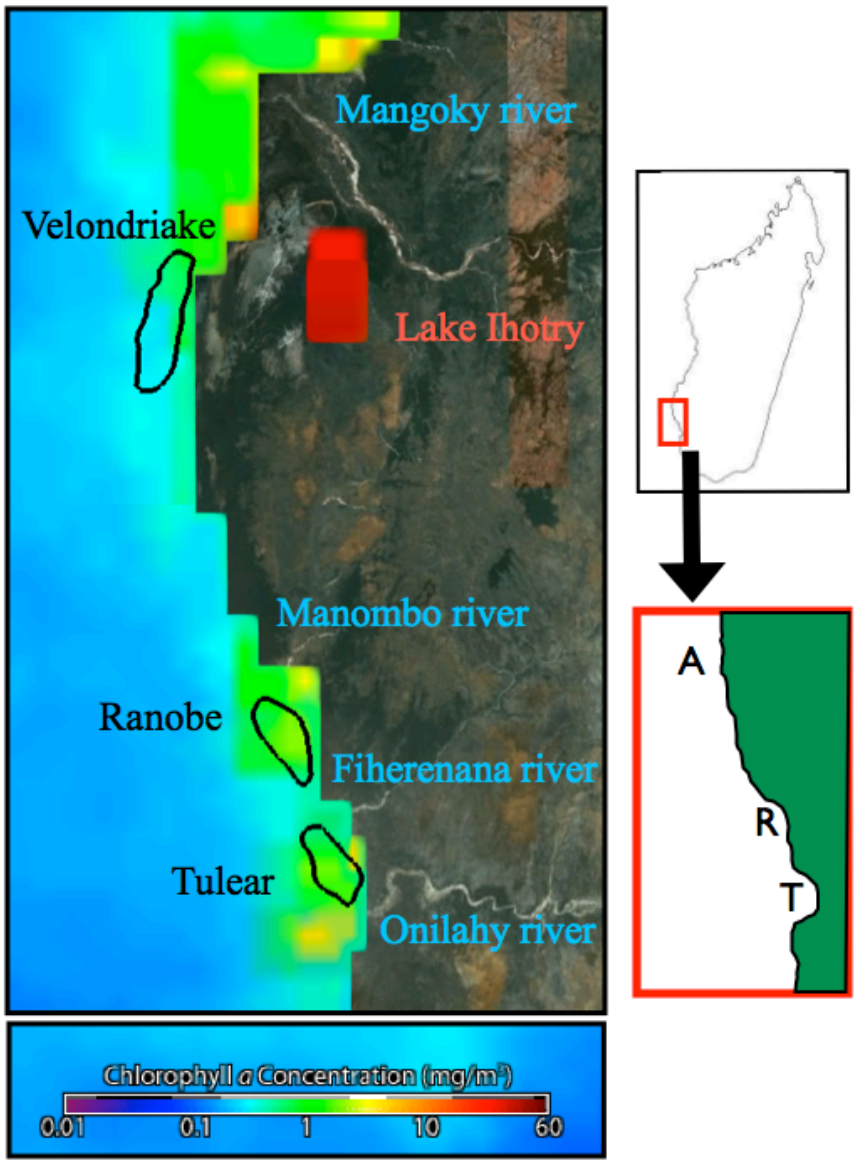


Figure 3.11 Chlorophyll *a* densities in the three study regions: Velondriake (black border farthest north), Ranobe (black border in middle), Tulear (black border farthest south). The chlorophyll density map was generated using real-time chlorophyll data from NASA's Goddard Space Flight Centre (GSFC) MODIS Aqua satellite. The image is based on real-time data accessed April 25th, 2012 and does not represent a long-term dataset. The uneven coastline is due to the resolution of the overlying chlorophyll density data layer (highest available). Note how the position of river mouth influences the overall density experienced by each study region. The red rectangle is Lake Ihotry, which experiences much higher chlorophyll levels than the coast.

3.3.7. Sea Surface Temperature (SST) and Degree Heating Weeks (DHW)

The degree heating weeks index (DHW), which combines the intensity and duration of thermal stress into "degree °C-weeks", shows how much heat stress has accumulated in the region over the previous 12 week period (NOAA, 2000). When thermal stress reaches around four degree °C-weeks, significant bleaching of sensitive coral species is common and by eight degree °C-weeks widespread bleaching and coral mortality is common (NOAA, 2011).

Sea surface temperature (SST) and DHW data for the three study regions were obtained from the NOAA Coral Reef Watch Satellite Monitoring dataset from 2000 to 2012 (NOAA, 2011). The resolution of the data is 0.5° x 0.5° or about 90 x 90 km at the latitude and longitude of the study sites.

Overall temperature regimes for the regions are similar (Figure 3.12). In 2006 and 2010 all regions reached four degrees °C-weeks from late February to mid-May. In 2006 bleaching potential decreased in the order Ranobe-Tulear-Velondriake and in 2010 Ranobe and Tulear had similar levels of thermal stress while Velondriake less so. This could indicate that the Velondriake region and the Tulear/Ranobe region are on either side of a region of oceanic temperature transition.

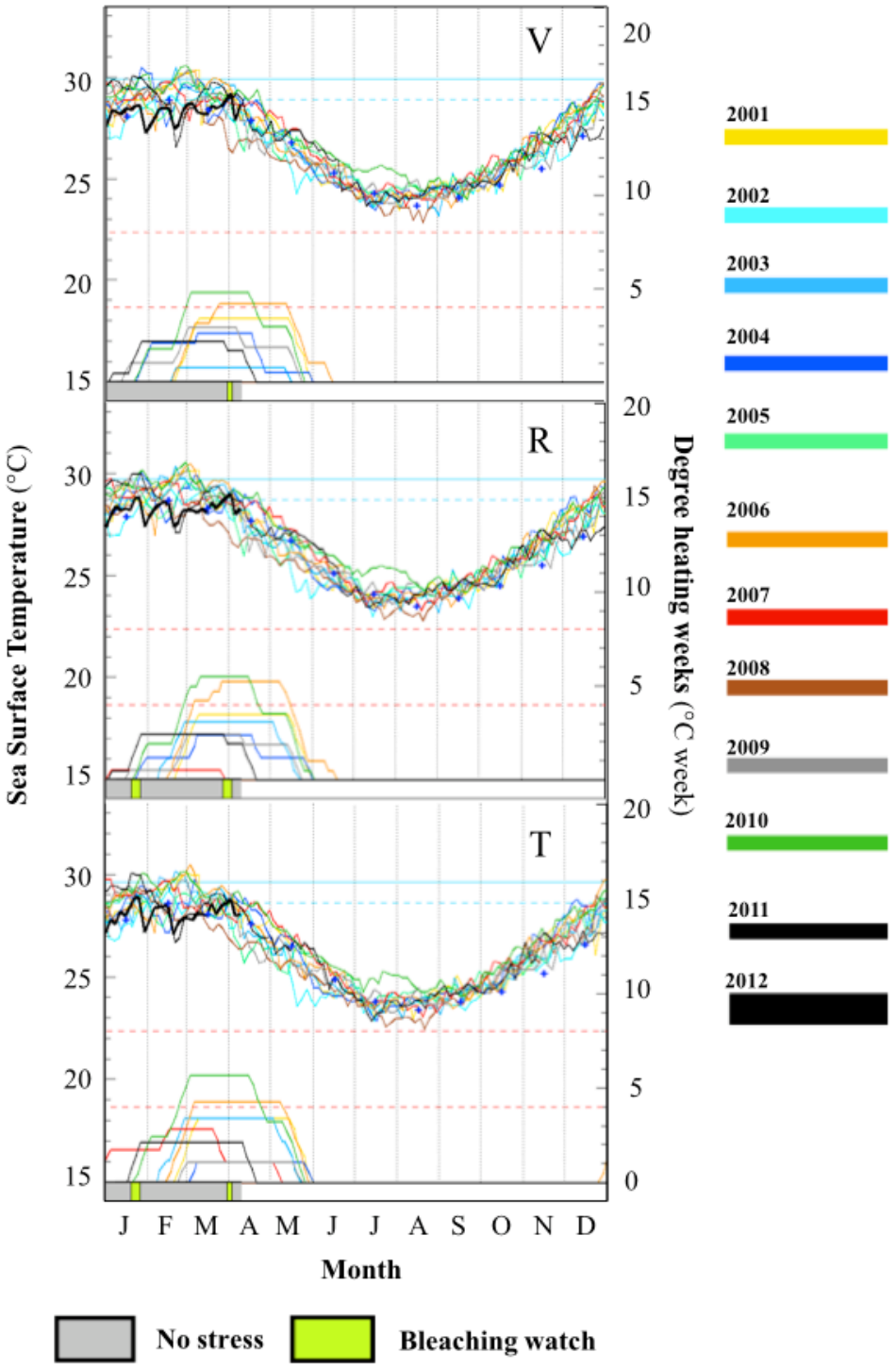


Figure 3.12 SST Bleaching weeks for the three study regions (V) Velondriake, (R) Ranobe, and (T) Tulear. Annual fluctuation in Sea Surface Temperature (SST) and Degree Heating Weeks (DHW) from 2001-2012. Figures were acquired upon request to NOAA Coral Reef Watch and then redrawn.

3.4. Coral Reef Types in Southwest Madagascar

Reef type is the result of many historical and existing abiotic factors including: antecedent geological platforms (sinking islands, local tectonic processes, uprisings etc.), salinity, sea level, and erosion of limestone by rain, waves, and storms (Sheppard et al., 2009). Reef morphologies are also due to historical and continuing biotic factors such as: 1) coral species community compositions which determine accretion rates, limestone densities, and small-scale reef morphology 2) boring organism community composition which influences erosion rates 3) herbivorous fish community composition which influences algal densities and thereby the spatial competition intensity that corals experience and 4) anthropogenic activities such as destructive fishing and diving practices.

The basic reef types and sub-types identified in the study regions result from many of the abiotic and biotic factors listed above. It is likely impossible to determine which factors impacted when and at what intensity to achieve the present typologies of reef sites. It is, on the other hand, reasonable to assume that reefs in Southwest Madagascar with similar shapes and 'types' (detailed later) have been exposed to similar historical and continuing environmental factors. Therefore reef typology is used as a proxy for similar historical environmental regimes. Here reef type is treated as an 'environmental factor' with the caveat that it is really a proxy for many historical environmental factors.

Basic geomorphological classification such as fringing reefs, patch reefs, and spur and groove systems were insufficient to adequately describe the 68 surveyed sites. The classic forms were expanded for the present purposes to six basic reef types and 20 sub-types based on reef morphology and other attributes.

In this section the major reef types and sub-types in Southwest Madagascar are presented. All plates referred to in this chapter are available in Appendix Two.

3.4.1. Coral reef types

3.4.1.1. Mound reefs (Type M)

The common feature of this reef type is the presence of mounded, solid, substrate with a surface structure that cannot be displaced by hand. The mounds are commonly between 0.5 and three metres tall with small or medium sand patches interspersed between the mounds in an irregular fashion. Large *Porites* bommies (*P. solida, P. lobata,* and *P. lutea*) commonly occur amongst the mounds.

Reefs with such mounded surfaces can be divided into five sub-types, which are summarized in Table 3.2. Type M1 consists of distinctly elevated patch reefs with obvious sloping edges (Appendix 2.1.1). Type M2 consists of non-elevated patch reefs that do not have distinct edges but rather taper off gradually into sparse mounds (Appendix 2.1.2). Type M3 consist of mounded areas with sand patches that form faint grooves, likely due to their exposure to the strong southern Madagascar current (Appendix 2.1.3). Type M4 consists of fringing reefs with a highly mounded surface structure (Appendix 2.1.4). Type M5 describes one unique reef site consisting of 15 metre tall pillars each about four metres in diameter with mounded surface structures (Appendix 2.1.5). These pillars are located in the south pass of the Ranobe barrier reef. Here the current is strong making fishing difficult, which may in part explain the relatively high coral cover found at this site.

Table 3.2 Reef types with a mounded surface structure. For each reef sub-type (M1-M5) a short description, reef sites, and the related Plate in Appendix Two is indicated.

Type	Description	Sites	Plate
M1	Mounded patch reefs with distinct edges	A19	2.1.1
M2	Mounded patch reefs without distinct edges	A3, A10-12, A15, A29-30	2.1.2
M3	Mounded reefs with faint sand grooves	A27, T12-13	2.1.3
M4	Mounded fringing reefs	A16-17	2.1.4
M5	Reef pillars	R16	2.1.5

3.4.1.2. Solid spur and groove systems (Type SG)

Spur and groove reef morphologies are well described and commonly occur on the seaward edge of barriers, which bear the brunt of incoming wave energy. The finger-like formations are likely due to erosion caused by swell and trade wind waves (Roberts et al., 1992). The size and shape of structures can be highly variable and is the basis for the classification used here (Table 3.3).

Table 3.3 Spur and groove reef types surveyed. For each reef sub-type (SG1-SG5) a short description, reef sites, and the related Plate in Appendix Two is indicated.

Type	Description	Sites	Plate
SG1	Shallow, narrow grooves with gently sloping spurs; grooves are not prominent features	R12-14, R23	2.1.6
SG2	Shallow and clearly defined spurs and grooves; grooves are prominent and regular features	A2, A22, R3, R11, R15, T2, T5	2.1.7
SG3	Steep, bulky spurs with short wide grooves	A13-14, T6	2.1.8
SG4	Deep canyon-like grooves	R24	2.1.9
SG5	Rubble spur and grove system	A4	2.1.10

Reef type SG1 is characterized by a gentle slope with shallow, narrow, meandering grooves, which are occasional, not prominent, features of the system (Appendix 2.1.6). Reef type SG2 consists of clearly defined shallow spur and grooves, which are often straight and directly perpendicular to the major current. SG2 spurs consist of non-motile substrate interspersed by small sand patches (diameter of 20 to 50 centrimetres) and vary from two to 25 metres in width while grooves range in depth from 0.3 to four metres (Appendix 2.1.7). SG2 grooves are filled with sand or rubble. SG3 reef types are characterized by bulky spurs that project bluntly like nubby fingers onto adjacent sand beds (Appendix 2.1.8). Often the spurs of such reefs have near vertical walls and deep grooves (three to five metres).

Reef types SG4 and SG5 were infrequent. Type SG4 is characterized by deep (12.5 metres) rolling canyon-like grooves more reminiscent of U-shaped valleys than grooves (Appendix 2.1.9). Type SG5 has low-lying spurs consisting of a framework of mainly branching coral rubble that has been solidified by coralline algae. The SG5 grooves are 0.5 to one metre wide, clearly defined, and filled with branching rubble hardened by coralline algae (Appendix 2.1.10).

3.4.1.3. Coral rubble fields (Type RF)

Most large patch reefs in the bay of Ranobe have deteriorated to extensive rubble fields. These systems (type RF1) consist of a meshwork of both branching and foliose rubble of various sizes (Appendix 2.1.11). These rubble reefs are shallow (1.5 to 5.6 metres) with relatively poor flushing, resulting in temperatures of 31-32 °C at the time of sampling. Heat stress along with destructive fishing practices have likely contributed to the structural collapse of RF1 reefs. Juvenile corals, *Fungia* spp. and *Porites rus* occur frequently on these rubble fields. At depths above two metres the reefs are often covered by fields of hardy and unpalatable *Turbinaria* sp. Structurally these reefs are unstable with surface rubble easily movable by hand.

In Tulear similar rubble fields occur vertically within the Bevata Vasque lagoon, which is located inside the Le Grande Récif barrier (RF2 reefs in Figure 3.19). Here rubble is so heavily laden with sediment that it is completely immersed towards the bottom of the lagoon and only just visible at shallower depths. Sediment tolerant attached species such as *Physogyra lichtensteini* and *Pavona cactus* along with freeliving species such as *Herpolitha limax* and *Halomitra pileus* dominate the lower reef slopes at ten to 15 metres (Appendix 2.1.12) while large stands of *Porites rus* (Appendix 2.1.13) and staghorn *Acropora* sp. (Appendix 2.1.14) dominate the crest and reef flat at three to four metres. The mid slope around five to ten metres is comparatively barren (Appendix 2.1.15).

Table 3.4 Rubble field type reefs (RF) present in the study regions. For both reef sub-types (RF1-RF2) a short description, reef sites, and the related Plates in Appendix Two is indicated.

Type	Description	Sites	Plates
RF1	Patch reef consisting of a meshwork of rubble	R5-6, R8-9	2.1.11
RF2	Rubble walls packed solidly with sediment	T3, T4	2.1.12-15

3.4.1.4. Coral walls (Type CW)

Coral walls (CW) are characterized by nearly vertical, relatively flat walls with a solid pavement foundation (Appendix 2.1.16). The walls plateau into a three to five metre wide strip of coral cover at the crest and then give way to algae, eelgrass and sand landward. Generally such walls have high coral densities and experiences strong currents.

Table 3.5 Coral wall type reefs (CW) present in the study regions. A short description, reef sites, and the related Plate in Appendix Two are indicated.

Type/Plate no.	Description	Sites	Plate
CW	Coral walls with a steep, flat, firm surface	A9, A28	2.1.16

3.4.1.5. Mounds and rubble reefs (Type MR)

The mound and rubble reefs (MR) described here are different from the mound reefs (M) described earlier in that they also feature rubble patches (Appendix 2.2.1) or rubble fields (Appendix 2.2.2) that are often dotted with *Fungia* spp., *Cycloseris* spp., and juvenile branching corals. The mounds of MR reefs consist of firm immovable substrate (see examples of mounds in Appendix 2.2.3-2.2.5) often comprised of either living or dead massive *Porites spp.* colonies partially overgrown by hard and soft coral, algae, and other benthic species.

The distribution of mounds and rubble on reefs are the basis for the classification of three MR sub-types (Figure 3.13 and
Table 3.6). Mounds and rubble areas exist as clearly separate zones on patch reefs (MR1; Figure 3.13) and fringing reefs (MR2; Figure 3.13) or they are interspersed with one another on patch reefs (MR3; Figure 3.13).

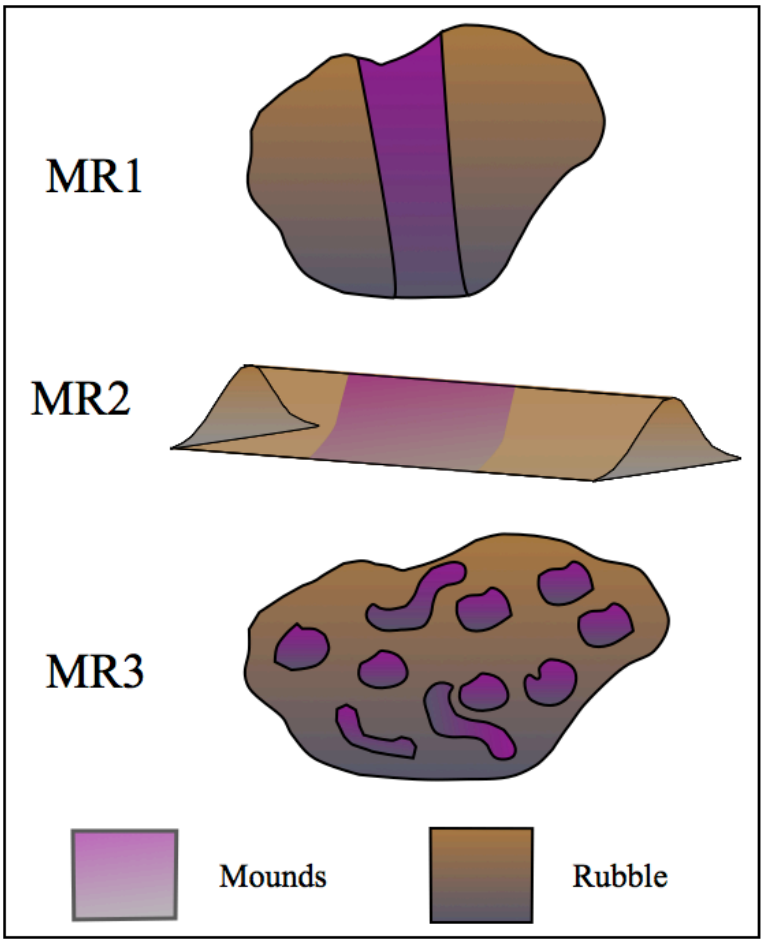


Figure 3.13 Generalized depiction of reef type: MR1 characterized as a patch reef with distinct zones of mounds and rubble, MR2 characterized as a fringing reef with distinct zones of mounds and rubble, and MR3 characterized as a patch reef with a mix of mounds and rubble throughout. Coral rubble is shown in brown and coral mounds are shown in purple.

Table 3.6 Reef types in the study regions dominated by mounded surfaces and coral rubble (MR type). For each reef sub-type (MR1-MR3) a short description, reef sites, and the related Figure and Plate in Appendix Two are indicated.

Type	Description	Sites	Figure; Plates
MR1	Patch reefs with clear zones of mounds and rubble	A23-25, R4	4.1; 2.2.2 - 2.2.5
MR2	Fringing reefs with clear zones of mounds and rubble	T14	4.1; 2.2.2 - 2.2.5
MR3	Patch reefs with a mix of mounds and rubble patches throughout	R10	4.1; 2.2.1,2.2.3-2.2.5

3.4.1.6. Mounds, monostand walls, and rubble (Type MMR)

Like the mound and rubble (MR) reef types the mound, monostand walls, and rubble (MMR) reef types contains mounds (Plate 2.2.3-2.2.5), rubble patches (Plate 2.2.1) and/or rubble fields (Plate 2.2.2). In addition the MMR reefs contain extensive monospecies stands, or monostands, that often form wall-like structures. In the case of *Pavona clavus* and *Galaxea astreata* monostands form two to four metre tall walls. Regardless of whether these monostands are dead or alive they form a specific type of structural habitat: stands of about ten centimetres wide coral heads approximately five centimetres apart. *Porites rus* and *Lobophyllia hemprichii* are also commonly found as extensive stands on MMR reefs, however, these do not form wall like structures.

The distribution of mounds, monostand walls and rubble on the reef are the basis for the classification of four MMR sub-types (Table 3.7). These three components can be mixed throughout a patch reef (MMR1; Figure 3.14) or fringing reef (MMR2; Figure 3.14). Alternatively these components can exist as clear zones on patch reefs (MMR3; Figure 3.14). In Ranobe and Tulear MMR3 reefs are usually covered with tall macro algae above 2.5 metres. Finally, patch reefs or inner segments of barrier reefs can have distinct zones of monostands, mounds (mainly *Porites* bommies), and rubble fields (MMR4; Figure 3.14). In Ranobe and Tulear this type of reef is usually covered with tall macro algae above 2.5 metres. Monostands usually consist of *Pavona clavus* (Appendix 2.2.6), *Lobophyllia hemprichii* (2.2.7), foliose *Montipora* spp. (Appendix 2.2.8), *Galaxea astreata* (Appendix 2.2.9), *Porites rus* (Appendix 2.2.10), and bushy *Acropora* spp. (Appendix 2.2.11).

Table 3.7 Reef types in the study regions dominated by variations of mounds, monostands and rubble patches. For each reef type (MMR1-MMR4) a short description, reef sites, and the related Figure and Plates in Appendix Two are indicated.

Type	Description	Sites	Figure; Plates
MMR1	Patch reefs with a mix of mounds, monostand walls and rubble patches throughout	A1, A5-8, A26	4.2; 2.2.1, 2.2.3-2.2.7
MMR2	Fringing reefs with a mix of mounds, monostand walls and rubble patches throughout	A20	4.2; 2.2.1, 2.2.3-2.2.5, 2.2.6-2.2.7,
MMR3	Patch reefs or inner segments of barrier with large distinct zones of mounds, monostands and rubble.	A18, A21, R1, R17, T8-11	4.2; 2.2.1-2.2.10
MMR4	Patch reefs or inner segments of barrier reef with distinct zones of monostands, mounds that are mainly *Porites* bommies and rubble fields.	R2, R7, R19-22, T7,	4.2; 2.2.1-2.2.10

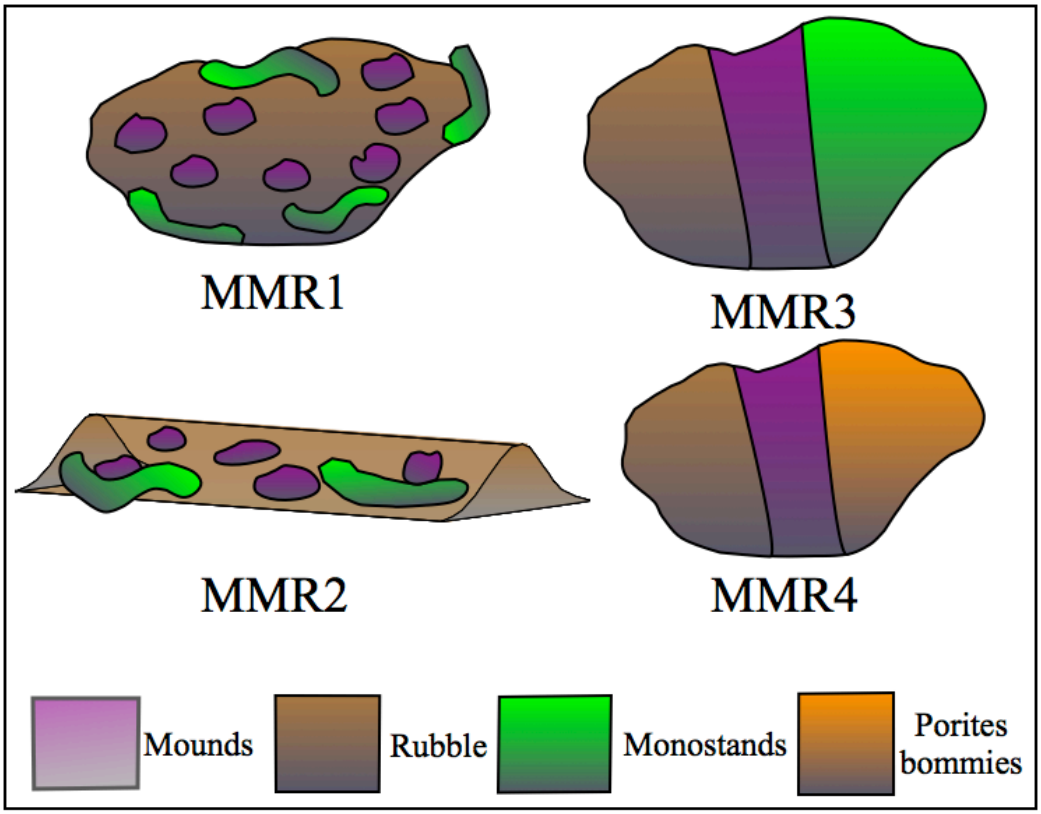


Figure 3.14 Diagram shows the generalized structure of the four types of MMR reefs which are characterized as follows: MMR1) patch reef with a mix of mounds, monostand walls, and rubble throughout, MMR2) fringing reef with a mix of mounds, monostand walls, and rubble throughout, MMR3) patch reefs with clear zones of mounds, monostand walls, and rubble and MMR4) is characterised as patch reefs or inner segments of barrier reef with distinct zones of monostands, mounds which are mainly *Porites* bommies and rubble fields.

3.4.2. Reef type location

3.4.2.1. Velondriake

In total 30 sites were surveyed in the Velondriake region (Figure 3.15). For clarity a separate map of the north (Figure 3.16) and south (Figure 3.17) are provided. The most common reef types were patch reefs with a mix of mounds, monostand walls and rubble patches (MMR1; 7 sites) and mounded patch reefs without distinct edges (M2; 7 sites). Sites outside the barrier were mainly spur and groove systems (SG), one of which was constructed entirely of branching coral rubble covered in coralline algae shaped into spurs (SG5). All major reef types (M, SG, CW, MR, MMR) could be found in the Velondriake region with the exception of rubble fields (RF), perhaps indicating that Velondriake has been less stressed than Ranobe and Tulear.

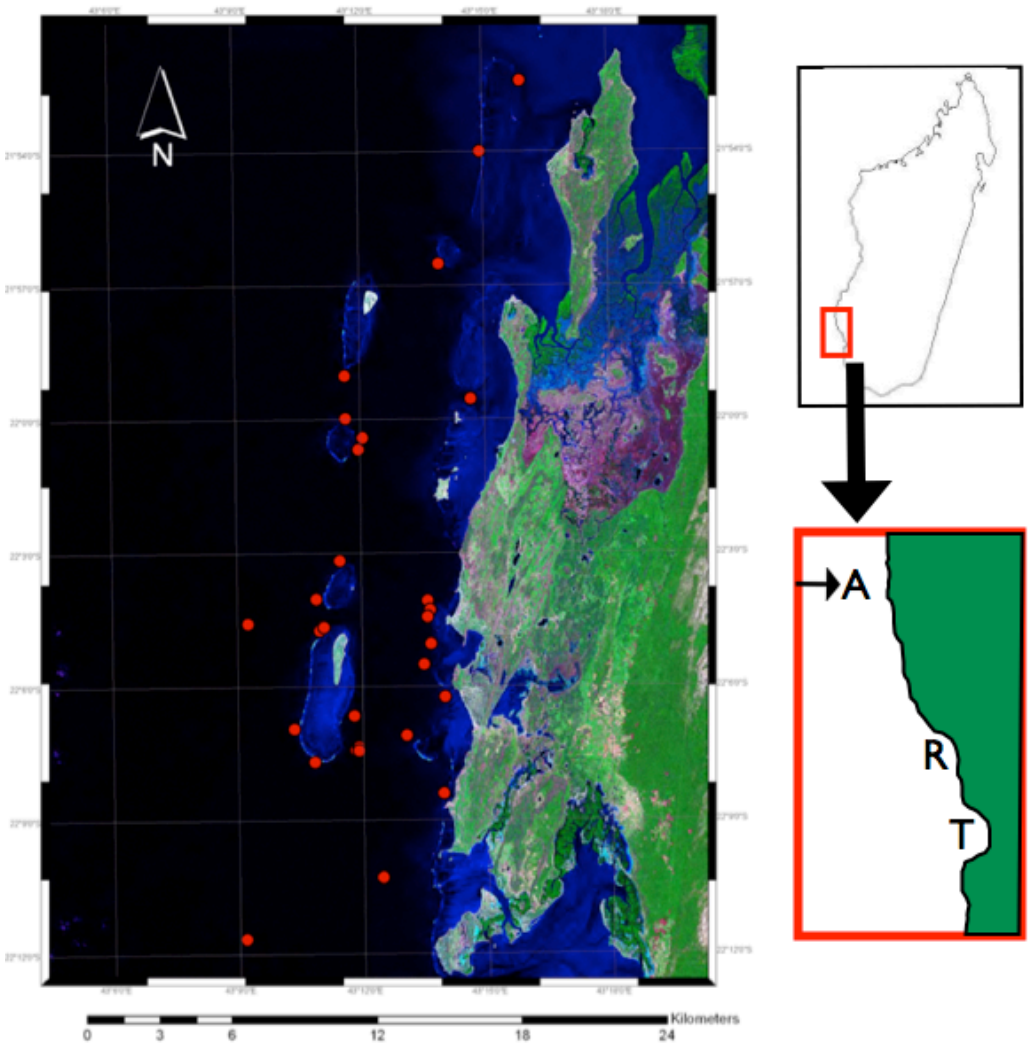


Figure 3.15 Overview of the entire Velondriake study region. Red dots indicate reef sites surveyed (30 in total).

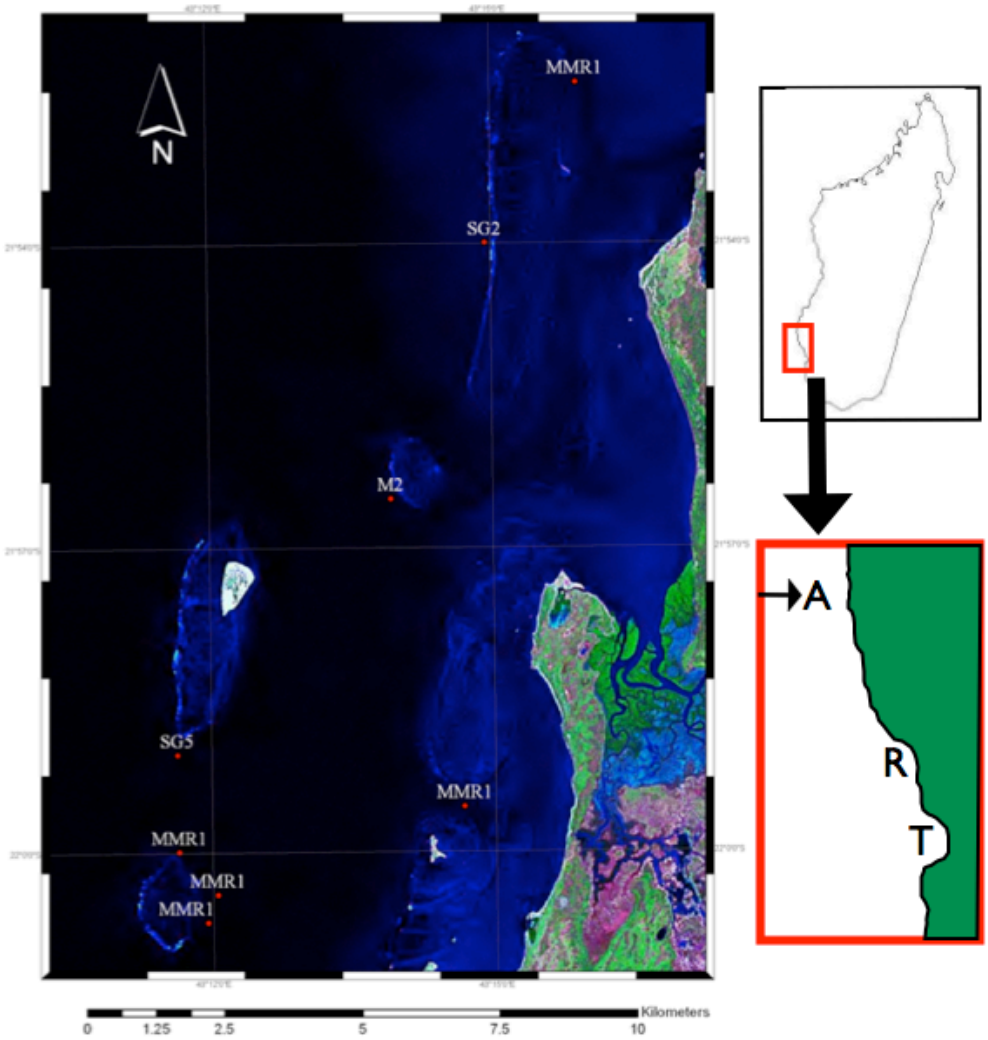


Figure 3.16 Reef types present in the north of the Velondriake study region (eight sites in total). Reef types are labelled with white text.

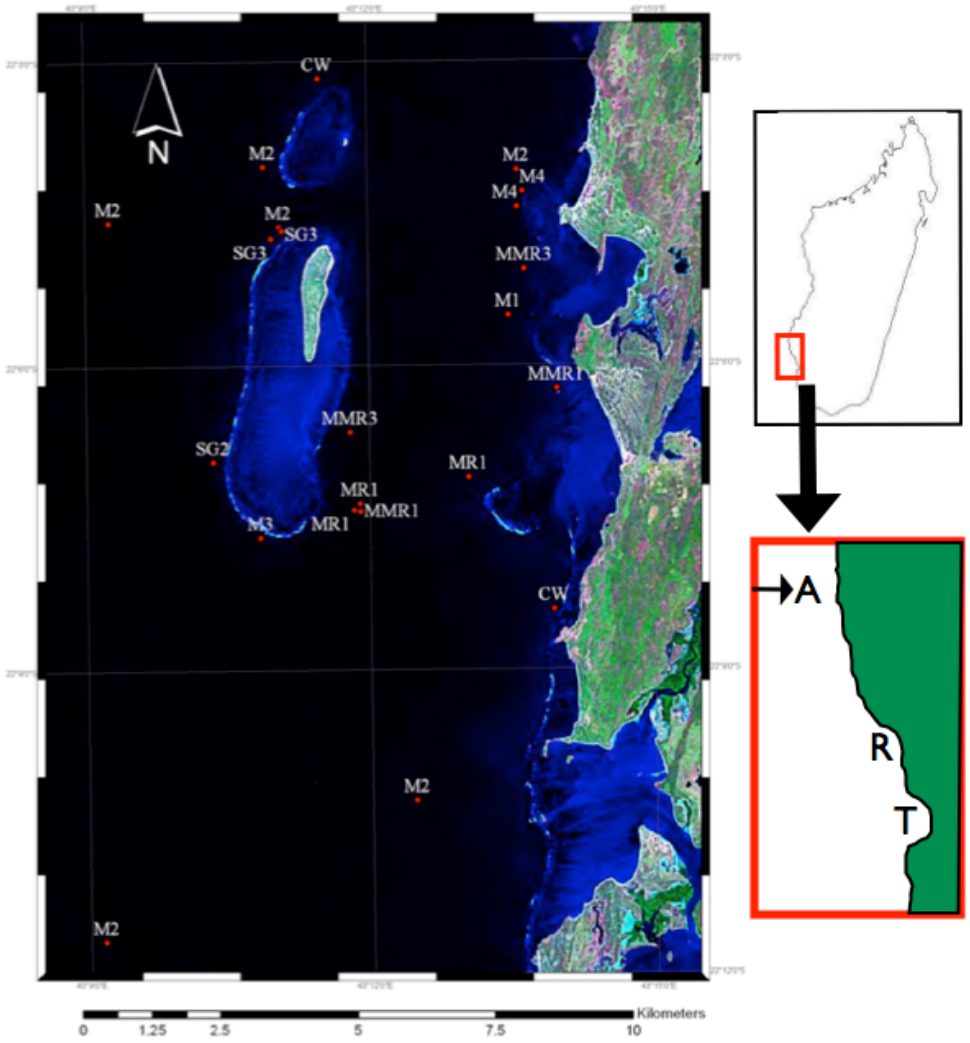


Figure 3.17 Reef types in the south of the Velondriake study region (22 sites in total). Reef types are labelled with white text.

3.4.2.2. Ranobe

In total 24 reef sites were surveyed in the Ranobe study regions (see Figure 3.18), however, one site was later dropped due to poor image quality. Outside the Ranobe barrier reef gently sloping spur and groove systems could be found with shallow, narrow, non-prominent grooves (SG1; four sites) or clearly defined straight grooves (SG2; three sites) or deep rolling canyon-like grooves (SG4; one site). Inside the barrier were mainly rubble fields (RF1; four sites) and reefs with distinct monostands, *Porites* bommies and rubble fields (MMR4; six sites) are found. In the south pass of the barrier are reef pillar formations (M5) with high coral cover, possibly due to the strong current experienced here which makes fishing difficult and flushes the reef with cooler waters. In the north pass of the barrier is a patch reef with clear zones of mounds and rubble fields (MR1).

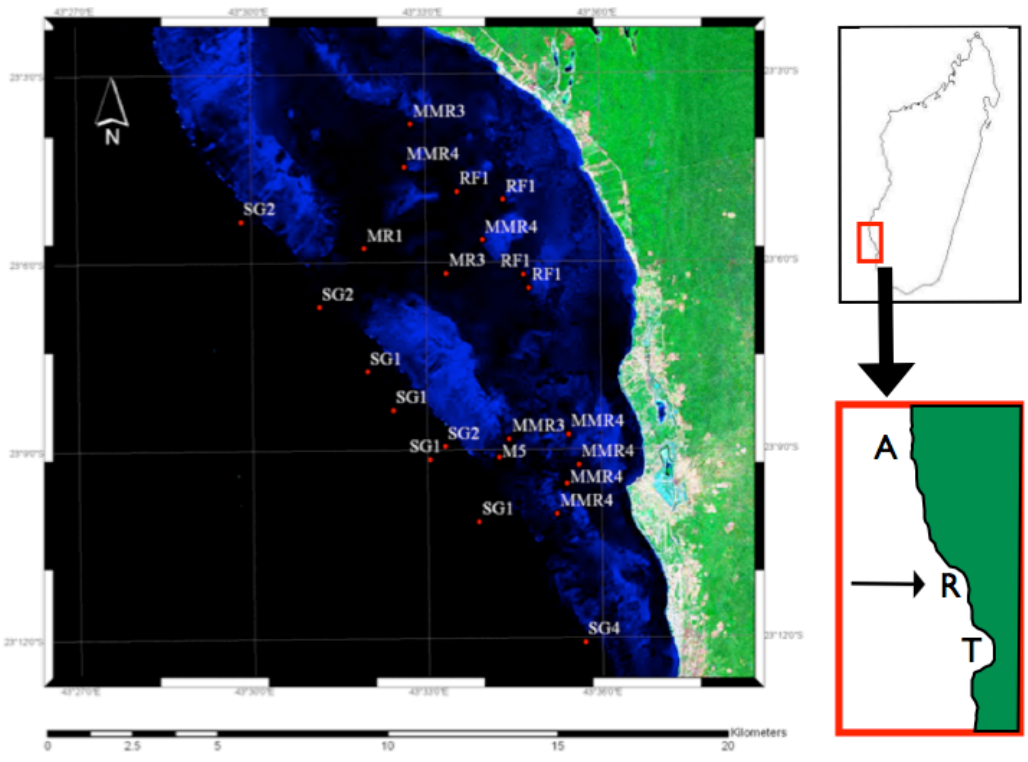


Figure 3.18 Reef types surveyed in the Ranobe study region (23 in total). Reef types are labelled with white text.

3.4.2.3. Tulear

In the Tulear study region (see Figure 3.19) gently sloping spur and groove systems can be found, with shallow clearly defined grooves (SG2; two sites) or steep, bulky spurs projecting onto a sand bed (SG3; one site). In the north section of the barrier a 15 to 20 metre deep lagoon can be found, locally known as 'Bevata vasque'. In this lagoon two rubble fields were found (RF2) that exhibited large free living coral colonies in the deeper sections and extensive monostands in the shallower sections. Along the inside the south section of the barrier and along several patch reefs in the south distinct zones of monostands, rubble fields and mounds (MMR4; four sites) or *Porites* bommies (MMR3; one site) were found. Two reef sites with mounds and faint sand grooves (M3) were found in the south pass of the barrier were the current is strong; these two sites had high coral cover. On a fringing reef outside the peninsula located in the south of Tulear bay, clear zones of mounds and rubble were observable (MR2).

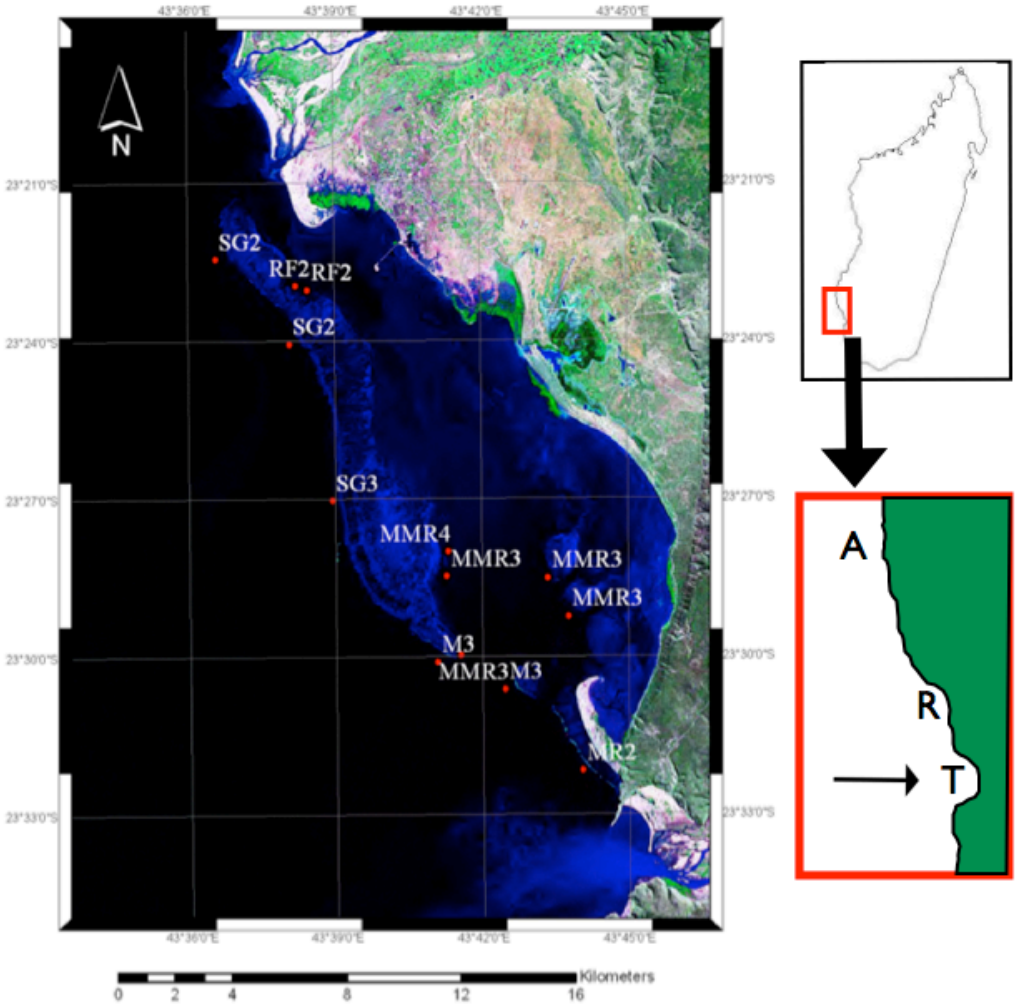


Figure 3.19 Reef types surveyed in the Tulear study region (13 total). Reef types are labelled with white text.

3.4.3. Summary

The six major reef types and 20 reef sub-types characterized for the three study regions are summarized in Table 3.8. These reef typologies will later be used as an 'environmental factor', with the caveat that they are really proxies for a plethora of current and historical environmental factors.

Table 3.8 Summary of reef types in Southwest Madagascar

Reef type	Reef Sub-type	Description
Mounded reefs	M1	Mounded patch reefs with distinct edges
	M2	Mounded patch reefs without distinct edges
	M3	Mounded reefs with faint sand grooves
	M4	Mounded fringing reefs
	M5	Reef pillars
Spur and groove	SG1	Shallow, narrow grooves with gently sloping spurs; grooves are not prominent features
	SG2	Shallow and clearly defined spurs and grooves; grooves are prominent and regular features
	SG3	Steep, bulky spurs with short wide grooves
	SG4	Deep canyon-like grooves
	SG5	Rubble spur and grove system
Rubble fields	RF1	Patch reef consisting of a meshwork of rubble
	RF2	Rubble walls packed solidly with sediment
Coral walls	CW	Coral walls with a steep, flat, firm surface
Mound and rubble reefs	MR1	Patch reefs with clear zones of mounds and rubble
	MR2	Fringing reefs with clear zones of mounds and rubble
	MR3	Patch reefs with a mix of mounds and rubble patches throughout
Mound, monostand, and rubble reefs	MMR1	Patch reefs with a mix of mounds, monostand walls and rubble patches throughout
	MMR2	Fringing reefs with a mix of mounds, monostand walls and rubble patches throughout
	MMR3	Patch reefs or inner segments of barrier with large distinct zones of mounds, monostands and rubble.
	MMR4	Patch reefs or inner segments of barrier reef with distinct zones of monostands, mounds that are mainly *Porites* bommies and rubble fields.

3.5. The Vezo people

Human settlement on Madagascar began around 2000 year ago and its population is ethnically highly diverse with origins in Malaysia, Africa, Arabia, and Europe. The Vezo ethnic group are an artisanal fishing people that reside on the Southwest coast of Madagascar. Vezo is the imperative form of the Malagasy verb mive, which means 'to paddle'. It also denotes the people and the local dialect found in the Southwest. The Vezo dialect is so different from the Malagasy spoken in the rest of the country that it is not understood by people visiting from inland. There is no official Vezo dictionary and some words tend to vary by village.

The Vezo define themselves more by their shared struggles against the sea than by ethnic origins (personal observation but see also Astuti, 1995). For example, after three weeks of paddling between reefs with my Vezo fishermen guides I was declared a *'ampela abo foty* Vezo', which directly translates to 'tall white Vezo girl'.

Traditionally the Vezo were distributed along an 80 kilometre long band around Tulear, but as fisheries in Tulear have largely collapsed (Harris et al., 2010), the Vezo find themselves forced to move northward to better fishing grounds. This migration has resulted in a gradient of fishing pressure decreasing from Tulear to the Velondriake region 200 kilometres north.

Plate 3.2 Vezo family and a '*ampela abo foty* Vezo' (see text).

3.6. Conclusion

In this chapter the three study regions and surveyed reef sites were introduced along with the rationale for their selection. Major environmental factors influencing the region were discussed including: large and small-scale bathymetry, major currents, wind systems and cyclones, tides, nutrient and sediment input by local rivers, and finally sea surface temperatures and degree heating weeks for the last decade. The geomorphological reef type of the reef sites was then presented along with a brief introduction to the local fishing people, the Vezo.

4.
Sampling coral diversity in Southwest Madagascar

4.1. Introduction

4.1.1. Sampling objective

The objective of sampling was to obtain coral species abundance and richness data that could be used to test the central thesis that coral life-history traits provide useful information beyond that gleaned from species composition data alone.

4.2. Methods

4.2.1. Sampling design

4.2.1.1. Target population

The target population was all *Scleractinian* corals present in the waters of Southwest Madagascar down to a depth of 35 metres. While species such as soft corals and algae were included in the survey, the target group for this study was *Scleractinian* corals as they provide the structural foundations of reefs and their traits (especially morphological traits) are central to both the provision of fish habitat and shoreline protection.

4.2.1.2. Reefs sampled

Reefs were sampled within ten kilometres of the shoreline of Southwest Madagascar between Tulear and Andavadoaka where the reef surface was located from the waters surface down to 35 metres depth.

4.2.1.3. Sampling unit

The most basic sampling unit of the survey was an identification point on a geo-tagged photoquadrat image of 64 x 86 cm (0.558 m^2); three points were identified on each image (Figure 4.1). The photoquadrats were positioned two fin kicks (roughly two to three metres) apart along survey transects that varied in length to

accommodate the size, shape and depth of the reef being surveyed (described further in subsequent sections).

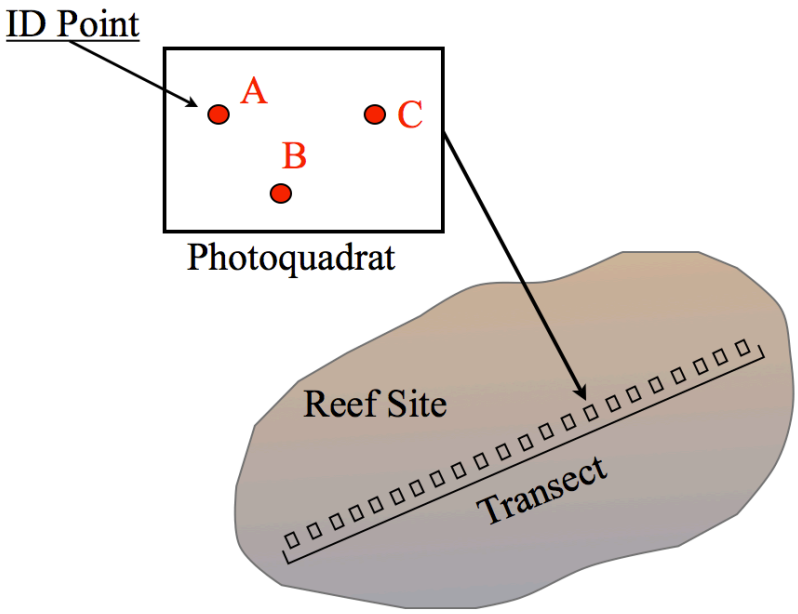


Figure 4.1 Sampling hierarchy used in the study. ID point "A" represents the most basic sampling unit, that is: one point on one photoquadrat image in one transect on one reef site.

4.2.2. Field sampling methods

Photo surveys were carried out from September 2009 to February 2010. Photoquadrat images were taken during dives in which standard scuba equipment was used. Images were taken at a distance of 46 cm from the reef surface, which was measured using a PVC pipe attached to a camera rig. A dive buddy or I towed a GPS floatation device throughout dives so that the position of each image could later be interpolated (Figure 4.2). The depth was recorded for each image by including a depth gauge (dive computer) in the corner of each image.

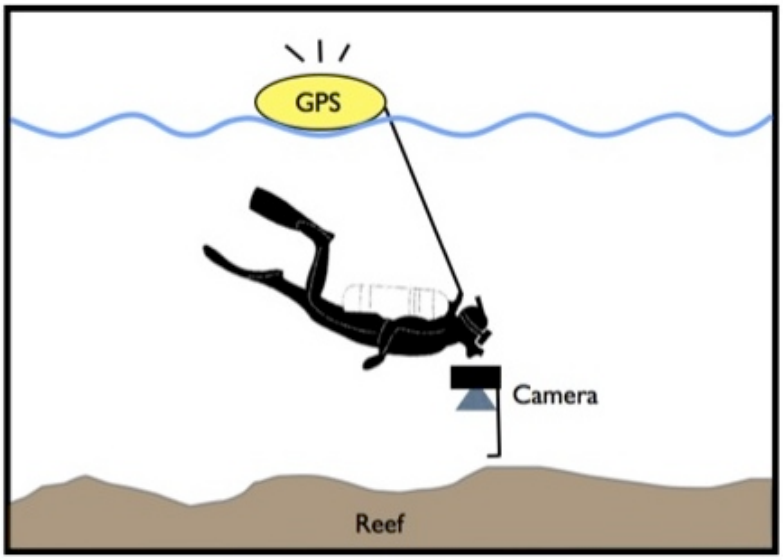


Figure 4.2 Overview of underwater sampling method. Images of the reef surface were taken from a known distance measured by a PVC pole attached to a camera rig. A GPS unit fixed to a floatation device was towed throughout the dive in order to record the position of each image taken.

4.2.2.1. Surveying Equipment

Photoquadrat images were taken with a Canon Ixus 980 IS digital camera placed into an Ikelite 60 metre housing, fitted with an Epoque DCL-20 46 mm wide-angle lens. The camera housing was mounted onto an extended AF35 tray with a 35 cm flex arm which was fitted with a Suunto SK-7 dive compass balanced for southern Africa (Figure 4.3). Mounting the compass onto the camera rig allowed for increased surveying efficiency compared to using a wrist-mounted compass, as it proved easier to maintain a given bearing.

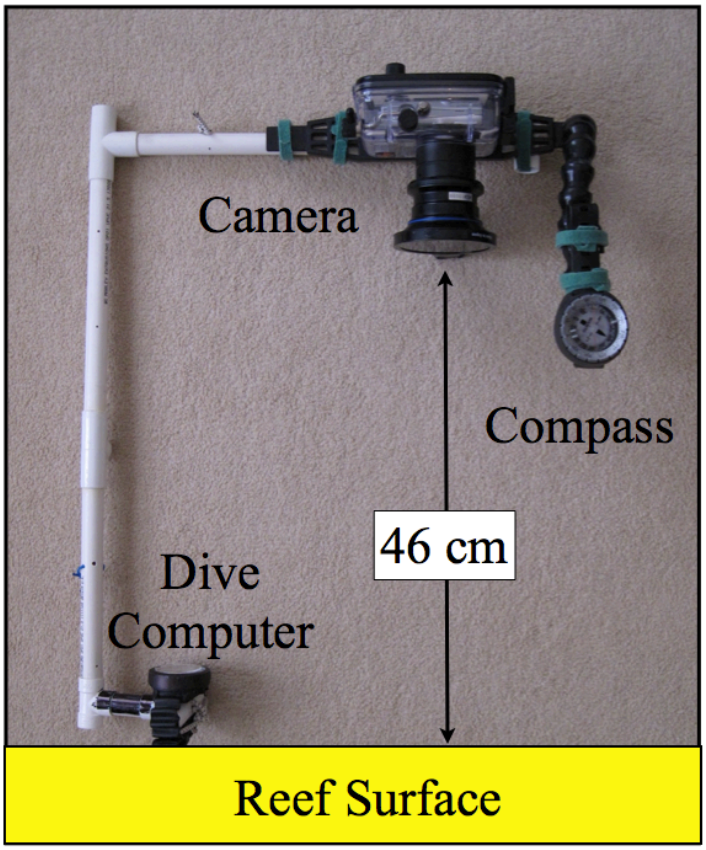


Figure 4.3 Camera set-up used during reef surveys. A Canon Ixus 980 IS in an Ikelite housing with a Epoque DCL-20 46mm wide-angle lens was mounted to a AF35 tray with a flex arm fitted with a compass. A Sunnto Gecko dive computer was fitted to a collapsible PVC pole used to gauge lens distance from reef surface.

To ensure that each photo included the same reef surface area, each photo was taken the same distance from the reef surface. To optimize surveying methods, a weighted string was initially used to measure the distance from the reef as per Roelfsema et al. (2007), but this method proved inadequate for any reef surface other than horizontal. A rigid but collapsible pole attached to the camera rig was used instead to maintain a standardized distance. The pole structure was created by running bungee cord through sections of PVC piping thereby allowing for easy assembly and disassembly under water. Small holes were drilled into the pipe to allow water to flow into the pipe displacing any trapped air. All joints where fixed with plumbers glue except one, which was left loose to allow for convenient storage on the boat and also for a smoother entry into the water (Figure 4.3).

A Suunto Gecko dive computer was mounted so that it appeared in the lower right hand corner of every image (Figure 4.8). This was done for three reasons: 1) to allow the author to be continually aware of the dive time and depth 2) to allow each image to be depth tagged so images from different sites but taken at similar depths could be compared and 3) it served as a scaling bar for each photo (the diameter of the computer face was exactly six centimetres).

The optimum distance from which to photograph the reef was found by testing a series of lens to reef surface distances ranging from 0.4 to two metres. It was found that a distance of 46 cm between the front of the lens and the reef surface was a good compromise between including enough reef surface area while maintaining a resolution at which coral species (or species cluster) identification would be possible even in poor visibility conditions.

The GPS flotation device consisted of a GPS unit (Garmin® eTrex Legend HCx) placed into a small Aquapac® which in turn was placed into a larger Aquapac® fitted to a surface marker buoy (SMB). In order to keep the SMB upright and ensure that accurate GPS data was being recorded a small weight was attached to the bottom of the SMB (Figure 4.4).

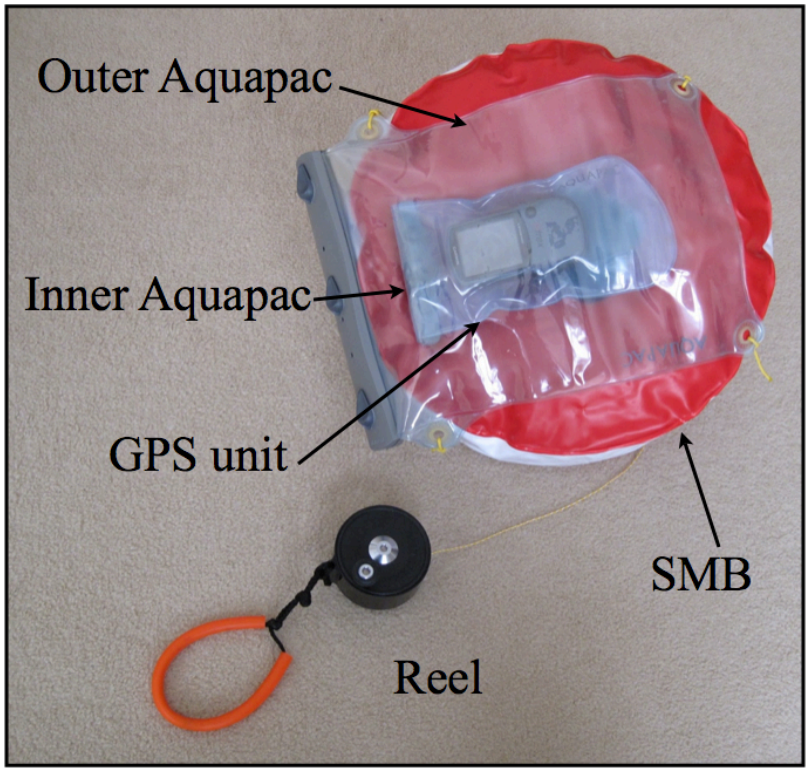


Figure 4.4 GPS float set-up: A Garmin® eTrex Legend HCx inside two Aquapac® drybags tied to a surface marker buoy (SMB) with a weight attached to the bottom to maintain the float in an upright position.

The camera housing was disassembled, cleaned and lubricated before and after each diving day to minimize the risk of flooding or malfunctioning.

4.2.2.2. Surveying protocol

At the beginning of each diving day a photo was taken of the clock on the Garmin eTrex Legend HCx GPS unit. This was done to record the time difference between the two devices and used to accurately geo-tag photoquadrat images later. Depending on the target reef survey sites either a motorized boat or pirogue (a Malagasy sailing outrigger canoe; see Figure 4.5) was used. GPS was used to navigate to the reef site when using the motorized boat. Local fishermen knowledge in combination with GPS technology was used to navigate to reef sites when using pirogues.

Figure 4.5 Traditional Malagasy pirogues were often used as transport to reef sites. A combination of GPS navigation and local fishermen knowledge were used to find ideal sampling sites.

For each reef site a survey form was completed recording: site name, survey date, start and stop time of dive, location of the site, geomorphological reef type (i.e. patch reef, fringing reef, or spur and groove), depth range of the area surveyed, latitude and longitude of the drop location for each site, air temperature, average water temperature, estimated wind speed (using the Beaufort wind scale), and cloud cover (as a percentage). In addition, if conditions and time allowed, a general area survey was done estimating the percentage cover of hard coral, soft coral, sand, rubble, fleshy and calcareous algae at the site. Notes taken during the dive recorded general and any distinctive or dominate features of the reef. The forms were printed on Durarite® underwater paper.

Survey dives commonly lasted 25 to 75 minutes depending mainly on depth. If the visibility allowed, the reefs were visually surveyed first for five to ten minutes in order to select the most representative areas of the overall reef habitat for sampling (next section).

4.2.2.3. Transect positioning

The number, length and pattern of transect positions depended directly on the size, depth, and geomorphology of the reef being surveyed. On small patch reefs, raised only a few metres from the seafloor, transects were positioned from one edge of the reef to another bisecting the near midpoint of the reef each time (Figure 4.6 A). This allowed the author to determine the total area of the reef. On large patch reefs with steep slopes this method was not possible due to diving constraints. Instead 'switchbacks' were conducted on one or both sides of the reef (Figure 4.6 B). On fringing reefs that ran along the coast or along barrier reefs, switchbacks were done if the reef was more than three metres deep, otherwise a single transect was conducted along the length of the fringing reef (Figure 4.6 C). These transects were often long (400 to 500 metres) as an entire shallow dive (70 to 75 minutes) was dedicated to just one transect. On spur and groove systems, transects were positioned perpendicular to the sand-filled grooves and the plateaus of the spurs were surveyed (Figure 4.6 D). If the grooves were deep and wide enough to safely fit into, then they were surveyed using switchbacks similarly to those conducted on large patch reefs (Figure 4.6 B).

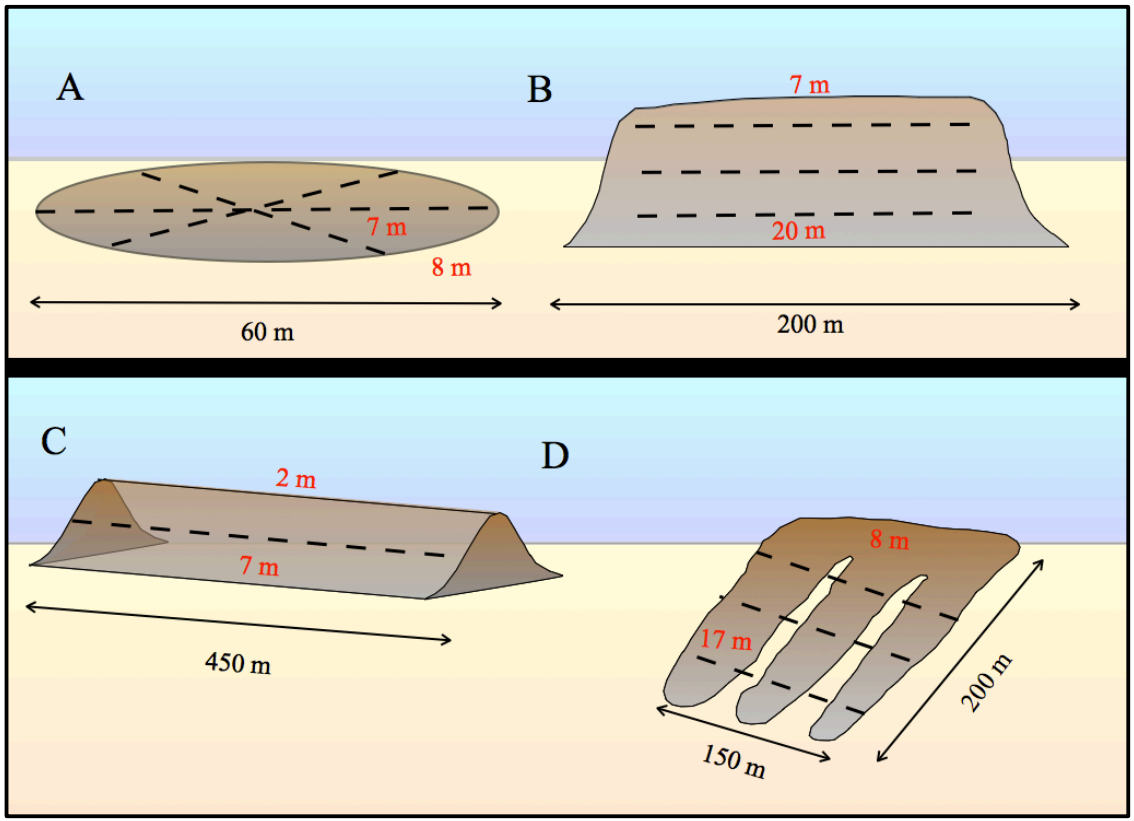


Figure 4.6 Positioning of transects (black dashed lines) on different reef geomorphologies (A-D). A) A small patch reef with a low relief (7-8 m). B) A large patch reef with a high relief (7-20 m). C) A long and shallow fringing reef (2-7 m). D) A spur and groove system (8-17 m). Examples of typical depths for reef types are indicated in red text while typical scales of the reef types are indicated using black double-headed arrows.

4.2.3. Image processing workflow

Images that were collected during field sampling were stored as .jpg images that were batch renamed in Adobe Bridge using the timestamp stored in the metadata of each image (i.e. yymmddhhmmss) and the site name at which they were taken (i.e. A1). The process of converting photoquadrat images to species abundance and richness data is summarized in Figure 4.7. In addition each image was examined visually and the depth recorded on the depth gauge in each image was included in the image name. The occupiers of three random points on each image were recorded using imaging software (Coral Point Count, NOVA Southern University Oceanographic Centre) that output data into a text file (.cpc file). A Unix shell script was written to extract and compile the required data into a master text file, which could subsequently be imported into R.

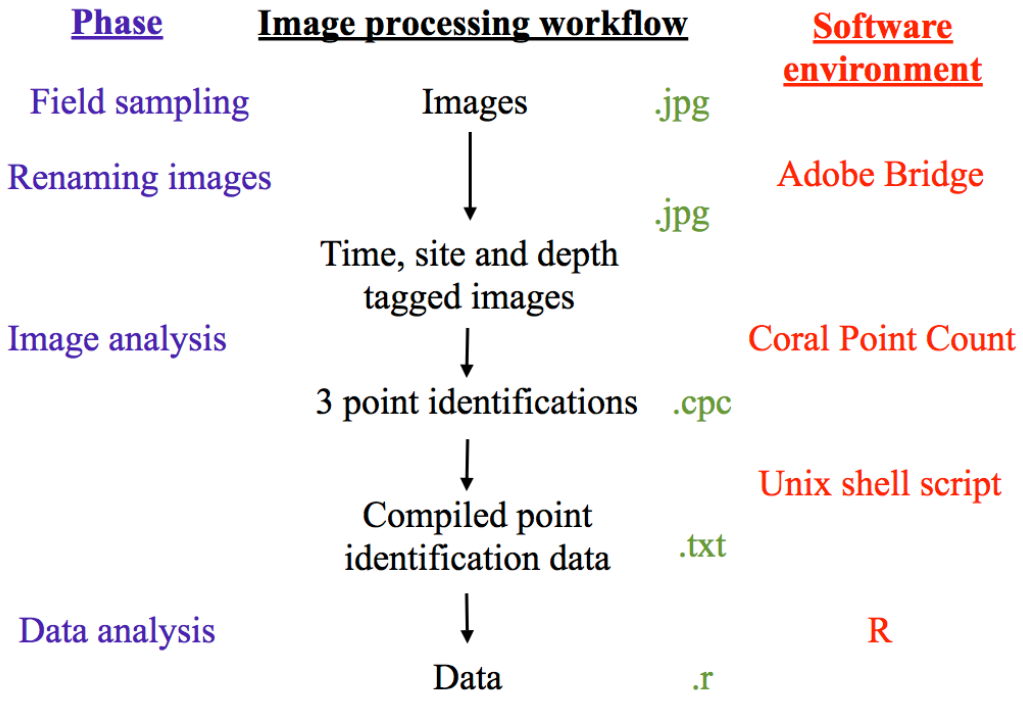


Figure 4.7 Overview of workflow for converting photo-transect images into species abundance and richness data. The file format of the data at each stage of the process is indicated in green.

4.2.3.1. Photoquadrat images

In total, 6,853 geo and depth-tagged photoquadrat images were collected at 68 different sites representing just over 200 km of coastline in Southwestern Madagascar. The images from one of these sites (R18) were of too poor quality to use while no coral could be identified at another (T1). The resolution of each image is high (14.7 megapixels) making it possible to identify corals to species level in most cases. Each of the photoquadrat images represents a 64 x 86 cm area (0.558 m^2) resulting in a total sample surface of 3,823 m^2.

4.2.3.2. Image pre-processing

At the end of each field-sampling day, images were downloaded and batch renamed using Adobe Bridge CS4. Each image was renamed using the timestamp stored in the metadata of each image (i.e. yymmddhhmmss) and reef site at which it was taken (i.e. A1). The depth that each image was taken at was then inserted into its name manually by examining the depth gauge reading visible in each image. Images were batch enhanced using the auto-tone, auto-contrast, and auto-color functions of Adobe Photoshop CS4. In addition, barrel distortion caused by the wide-angle lens was corrected in each image using PTLens, a Photoshop plugin and stand-alone program developed by Tom Niemann (epaperpress.com/ptlens). Personal communication with the PTLens developer was instrumental in fine-tuning the settings.

4.2.3.3. Quantifying the data using Coral Point Count

After preprocessing the benthic composition was quantified using Coral Point Count with excel extension software (hereafter CPCe; Kohler and Gill, 2006). CPCe allows for estimation of benthos community statistics using a random point count method on still images. This method involves overlaying a matrix of randomly distributed points on an image and identifying the underlying species or substrate type visually (Figure 4.8). Point identifications are recorded using category codes; in this study 223 category codes were used. Category codes are input into CPCe using a code file. The code file used for point identification can be found in Appendix Three and lists all *Scleractinian* species-level, *Scleractinian* cluster-level, non-*Scleractinian* species

categories and substrate categories used in the study. The code file is available as a .txt file in Digital Supplement 1.2.1.

For each image analysed a short .cpc file is created which is intended to be combined with other .cpc files into an excel file by CPC with summary statistics for the site. Initially, the coverage data from each site .xls file was pasted into a master .xls spreadsheet. However, it was found later that a far more efficient workflow is achieved by extracting and combining data into a text file independently using a Unix shell script (available as Digital Supplement 1.2.2) and then importing the data into R.

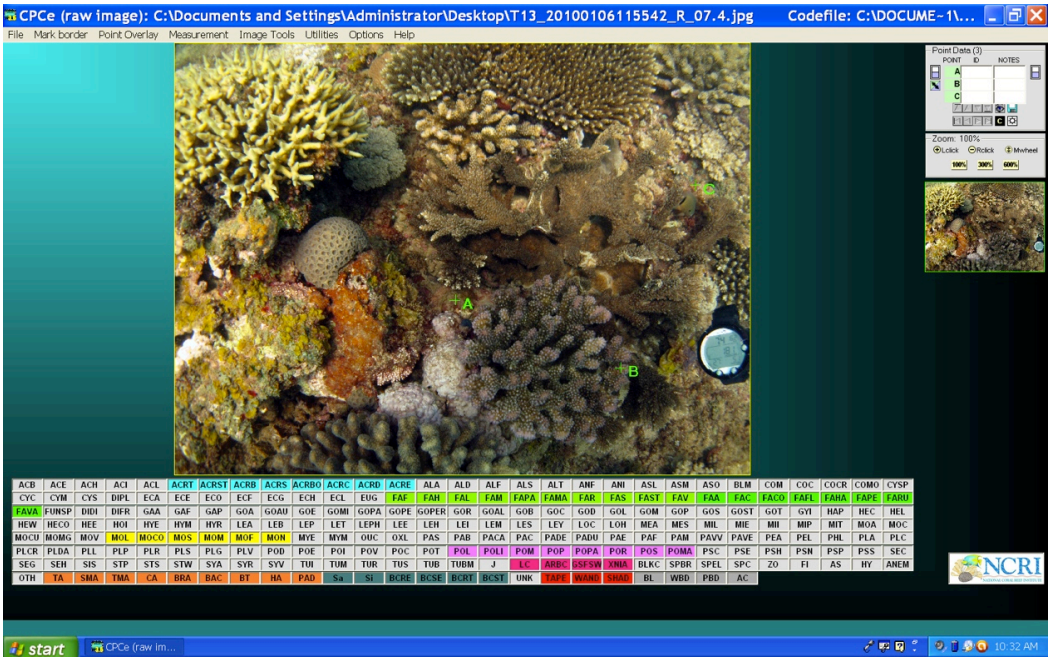


Figure 4.8 Example of the Coral Point Count Software (CPCe) user interface. The photoquadrat image is located at the centre of the screen and the depth gauge can be seen in the lower right-hand corner of the image. Three random points are scattered on the image (green text A-C). The boxes at the bottom of the screen each refer to a coral species, a coral species cluster, or another point occupier (i.e. algae, zooanthids, rubble). The grey box in the upper right hand corner indicates what point identification was made for each of the three points and will be output in the cpc file.

4.2.4. GPS Processing workflow

For each site surveyed, the track travelled under water whilst photographing the reef was recorded using a GPS unit fitted to an SMB pulled along the surface throughout

the dive. The GPS unit recorded positional information every five seconds for the duration of the dive. GPS-Photo Link GIS Pro Software was used to match each image to the nearest available GPS point recorded. A photo of the GPS receiver was used as the method of time synchronization. The image was matched to the closest available GPS point and coordinates were only used if recorded within ten seconds of the image time.

The process of linking the GPS data collected during field sampling to photoquadrat images and then importing this data into a database is summarized in Figure 4.9. GPS data was downloaded in .gpx format directly into a geo-tagging software platform (GPS-Photo Link) where the timestamps of the GPS coordinates and photoquadrat images were used to match the two. The photo-linked GPS data for each site was then exported as .csv files, subsequently labelled with their respective site number and compiled into a master .csv file using a script written in Python 2.7. The master photo-linked GPS data file was then imported into R.

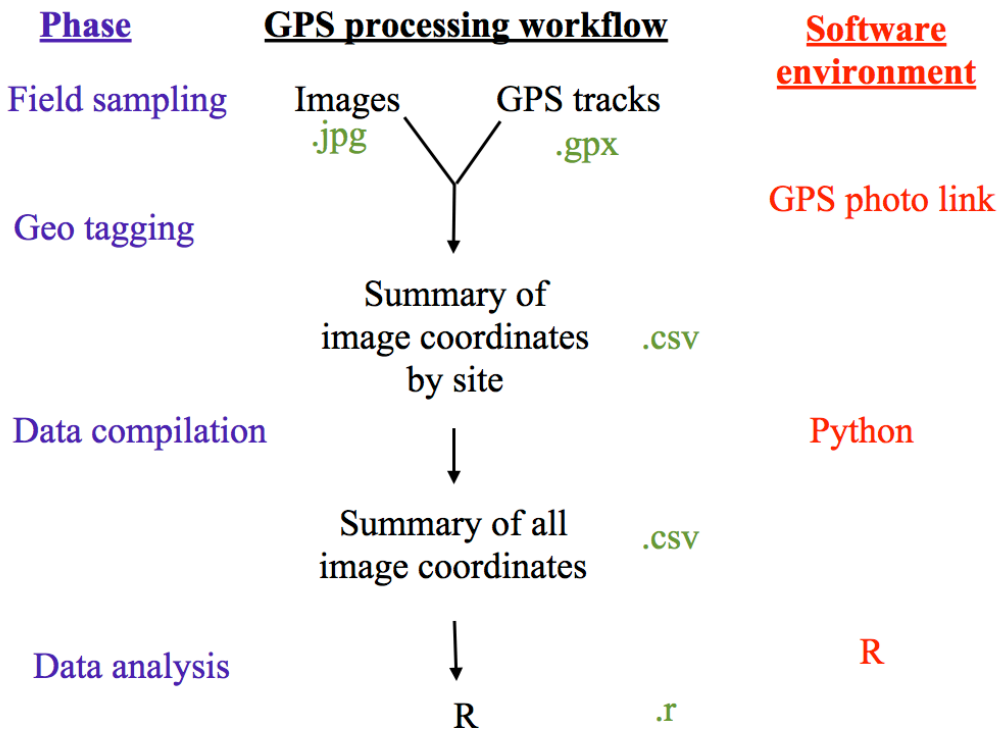


Figure 4.9 Overview of workflow for linking GPS coordinates from tracks collected during the field survey to photo-transect images and then importing them into the database. The file format of the data at each stage of the process is indicated in green.

4.3. Species clusters

A central aim of this dissertation is to compare if and how measurement of diversity and abundance of species and traits differ in the information they convey about reef sites. To examine this question both the species and trait abundance for reef sites are measured, which in turn requires coral species-level identification. This is not possible in all cases as some species are difficult to distinguish. To address this, a methodology was developed to generate a species-abundance matrix for reef sites even when species-level identifications could not be made for some species. The purpose of this section is to describe this methodology.

4.3.1. Ecoregion 16

While species-level identification was not possible for some species, genus-level identification and colony morphology was always possible to identify. This information in combination with information about the biogeographic distribution of species could then be used to generate a list of 'possible species' for a particular genus and colony morphology, such a group is hereafter referred to as a species cluster. In this sub-section the biogeographic data used to create species clusters is discussed.

The biogeographic data used was taken from the spatial database *Coral Geographic,* based on 798 species distribution maps that have been divided into 141 ecoregions (Veron et al., 2011). The maps in *Coral Geographic* include verified published occurrences of each species in each ecoregion. The original data used to generate the ecoregion maps are taken from two key sources: revised species distribution maps from Veron (2000) and species complements resulting from fieldwork conducted by Veron, DeVantier, and Turak, in 83 of the 141 ecoregions (as of November 2011).

An ecoregion is an area that exhibits a relatively homogeneous species composition that can be clearly distinguished from adjacent systems. Ecoregions are often defined by a small number of ecosystems and/or distinct oceanographic or topographic features. While the biogeographic forcing agents may vary between ecoregions they often include: isolation, upwelling, nutrient inputs, freshwater influx, temperature

regimes, exposure, sediment levels, currents, and bathymetric and coastal complexity (Spalding et al., 2007). Overlaying the ecoregions and currents present around Madagascar reveals that one of the major biogeographic forcing factors is the currents and shape of the coastline (see Figure 4.10).

The three study regions (Velondriake, Ranobe, and Tulear) are located in *Coral Geographic*'s Ecoregion 16 (see Figure 4.10) so one can assume that the biogeographic distribution of coral species in the three study regions are similar. Therefore the same ecoregion species list was used to generate the species clusters for all three study regions.

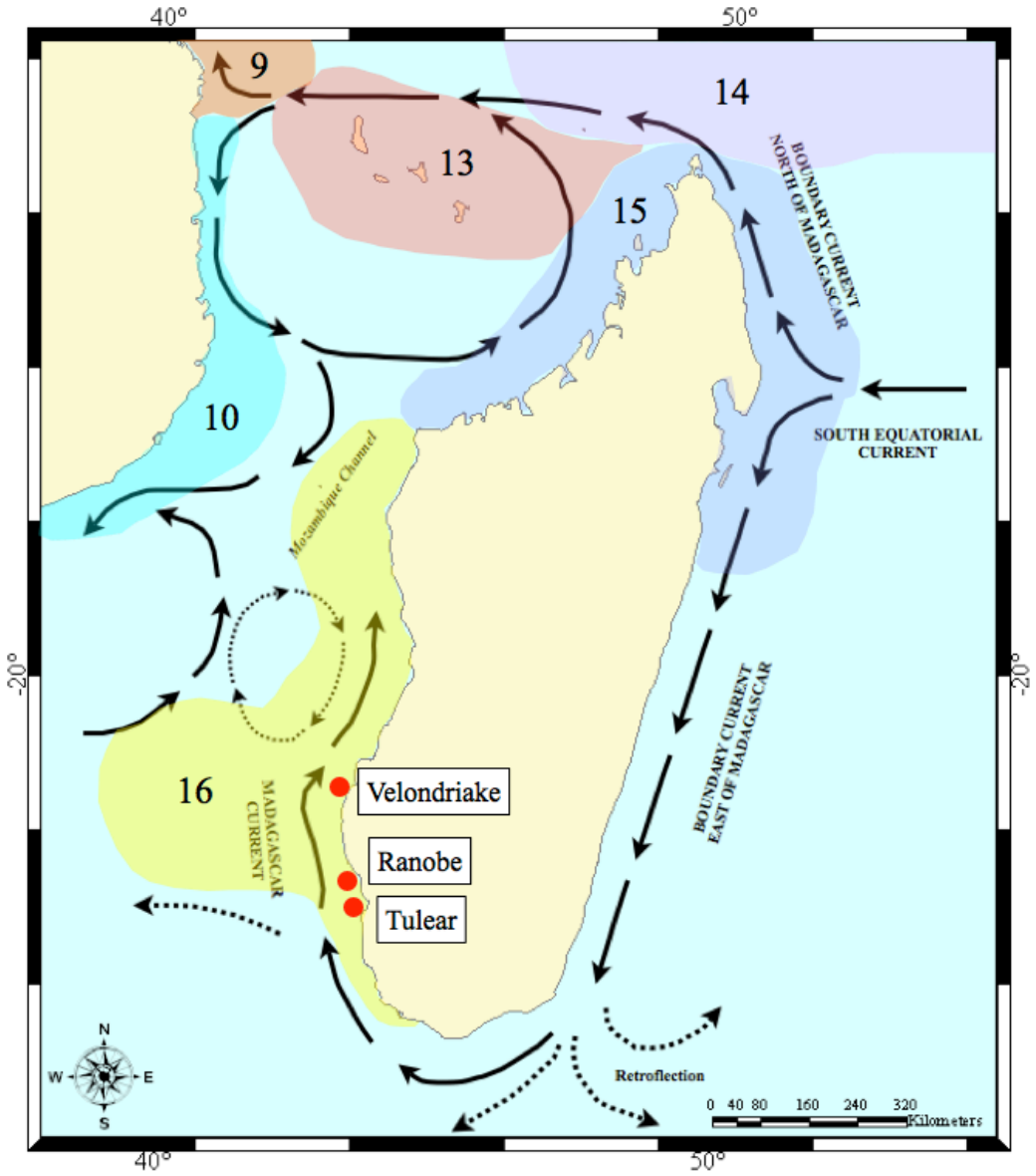


Figure 4.10 Ecoregions from the Coral Geographic database. The study regions are marked with red points. Note that all three study regions fall within the same ecoregion and can therefore be assumed to have biogeographically similar species distributions. It is highly likely that one of the major biogeographic forcing agents for the ecoregions present around Madagascar are the currents (marked with black arrows on the map).

4.3.2. Species Cluster Overview

It is sometimes difficult to distinguish between species within the genera *Montipora*, *Acropora*, *Fungia*, *Cycloseris*, and massive *Porites*. For these genera, species from

underwater photographs were grouped into 'clusters'. Where this is the case, cluster membership and trait variation between species in each cluster is discussed.

In total 114 individual coral species and 14 coral species clusters possibly representing up to 117 individual coral species (explained in the following section) were identified during the survey, representing a maximum of 231 species. The five genera for which species clusters were used also contained the greatest species richness (Table 4.1) and abundance (Figure 4.11).

Table 4.1 Summary of the number of species by genus present in the survey. In five genera (red text) species that were difficult to tell apart were lumped into species clusters to avoid misidentification.

Genus	**Species count**	**Genus**	**Species count**
Acropora	64	*Herpolitha*	2
Montipora	27	*Hydnophora*	2
Fungia	15	*Mycedium*	2
Porites	9	*Psammocora*	2
Cycloseris	8	*Symphyllia*	2
Favites	8	*Turbinaria*	2
Favia	7	*Blastomussa*	1
Goniastrea	7	*Coscinaraea*	1
Goniopora	6	*Diploastrea*	1
Pavona	6	*Gardineroseris*	1
Platygyra	5	*Halomitra*	1
Echinopora	4	*Leptoria*	1
Leptastrea	4	*Lobophyllia*	1
Pocillopora	4	*Merulina*	1
Alveopora	3	*Oulophyllia*	1
Astreopora	3	*Oxypora*	1
Cyphastrea	3	*Pachyseris*	1
Leptoseris	3	*Pectinia*	1
Montastrea	3	*Physogyra*	1
Seriatopora	3	*Plerogyra*	1
Stylophora	3	*Plesiastrea*	1
Acanthastrea	2	*Podabacia*	1
Echinophyllia	2	*Polyphyllia*	1
Galaxea	2	*Siderastrea*	1
Total	**201**	**Total**	**30**

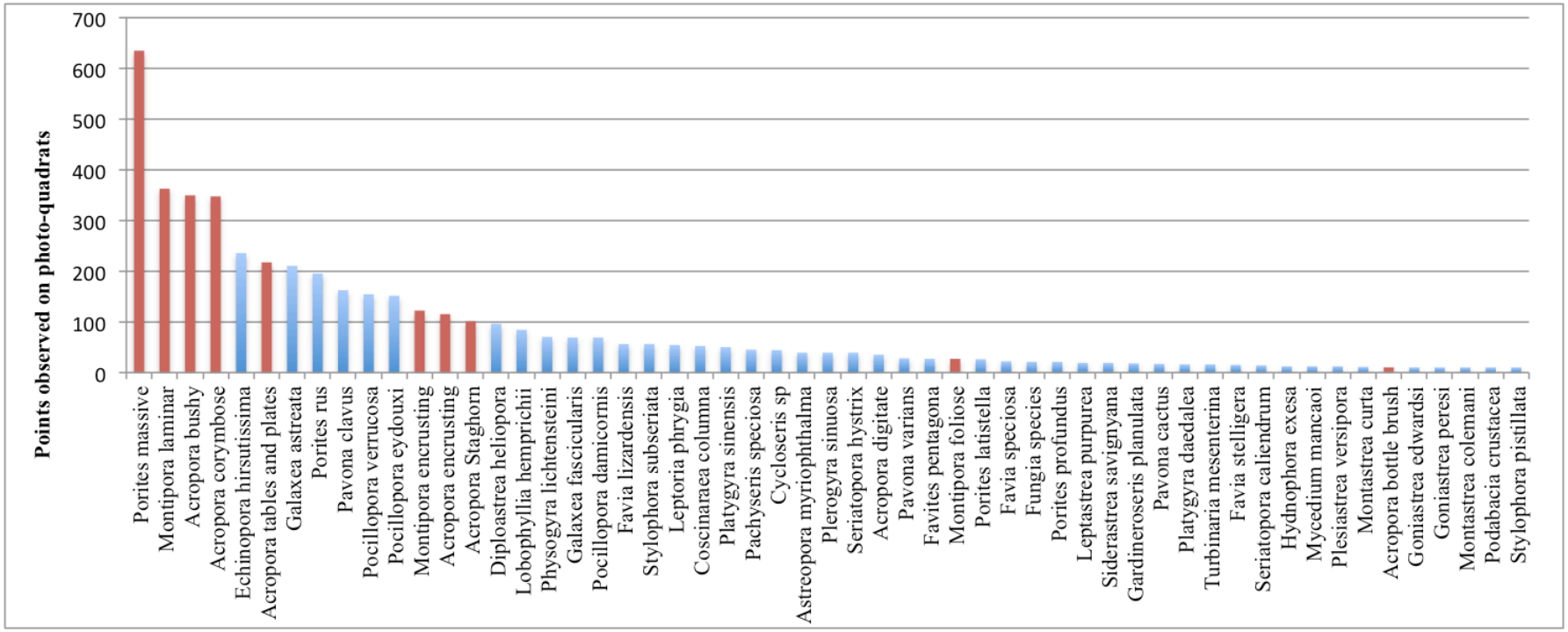


Figure 4.11 The overall abundance of species (blue bars) and species clusters (red bars) for the 4, 895 coral points identified in the study.

The genera: *Montipora, Acropora, Fungia, Cycloseris*, and massive *Porites* species were divided into species clusters. In total, 117 species were divided into 14 clusters spanning five genera (see Table 4.2).

Table 4.2 Genera for which species clusters were used, and the number of clusters and species per genera.

Genus	**No. Clusters**	**No. Species**
Acropora	7	64
Montipora	4	27
Fungia	1	15
Cycloseris	1	8
Porites	1	3
Total	**14**	**117**

4.3.2.1. Commonality of species within clusters

Species within the species clusters are not equally common within the study regions. Veron (2000) gives a generalized description of abundance identifying each coral as being common, sometimes common, uncommon, or rare. Carpenter et al. (2008) published a list that contained, among other things, generalized global abundances for corals. This list was compared against Veron's and it was found to agree in all but two cases: Carpenter et al. listed *Acropora samoensis* and *Acropora austera* as being 'common', while Veron listed both as being 'usually uncommon'. In these two cases Veron's classification was used (summarized in Appendix Five).

To avoid having to average the trait values for the species within a species cluster, each species cluster observation was replaced by a species from within the cluster by weighted random selection. The weighting used in this selection process (Table 4.3) was assigned using Veron's commonality classification described above.

Table 4.3 Weighting of species within species clusters for weighted randomization based on global abundance

Global abundance listed by Veron (2000) and Carpenter et al. (2009)	**Weighting**
Common	0.55
Sometimes common	0.3
Uncommon	0.1
Rare	0.05
Total	**1**

4.3.2.2. Replacing species clusters observations with species names

The trait similarity within the genera *Acropora, Montipora, Fungia, Cycloseris*, and *Porites* are similar enough to stand out as emergent groups (demonstrated in the following chapter). However, on a finer scale (i.e. weighting all trait attributes equally) it is clear that while these groups have high levels of trait similarity, they are not identical. To ensure that these minor trait differences were accounted for in the analysis each recorded observation of a species cluster (i.e. massive *Porites*) was replaced by a species from within the species cluster (i.e. *Porites solida*). The replacement method was coded in R; the annotated script is available in the Digital Supplement 1.3. Briefly, each time a species cluster observation is encountered, a species within that cluster is randomly selected but this choice is weighted by the global commonality of the species as listed by Veron (2000). The resulting site-species abundance matrix was used in calculating site similarity in terms of both species and traits (Chapter Six).

The species membership and trait variability within each cluster is discussed in the following sections.

4.3.3. Acropora Clusters

Sixtyfour species of *Acropora* occur in Ecoregion 16 (Veron et al., 2011), their global commonality is summarized in Table 4.4.

Table 4.4 Summary of *Acropora* commonality for Ecoregion 16

Global abundance listed by Veron (2000) and Carpenter et al. (2008)	***Acropora* Species present in Ecoregion 16**
Common	32 (50%)
Sometimes common	8 (12.5%)
Uncommon	19 (29.7%)
Rare	5 (7.8%)
Total	**64 (100%)**

Coral species within *Acropora* exhibit plasticity in colony morphology along environmental gradients such as light, sedimentation, and wave exposure (reviewed by Todd, 2008). Nevertheless they still tend towards one 'native' growth form, which are used as the basis for the clusters (Table 4.5). The *Acropora* clusters are described in more detail in the following sections.

Table 4.5 Cluster membership of the 64 *Acropora* species known to have biogeographic distributions overlapping the three study regions.

***Acropora* cluster**	**No.**	***Acropora* species in cluster**
Encrusting	2	*A. palifera, A. cuneata*
Staghorn	6	*A. copiosa, A. formosa, A. grandis, A. microphthalma, A. nobilis, A. pulchra.*
Bushy	18	*A. abrotanoides, A. austera, A. brueggemanni, A. florida, A. hemprichii, A. inermis, A. loripes, A. pinguis, A. robusta, A. rosaria, A. roseni, A. squarrosa, A. striata, A. valida,* and *A. variabilis, A. variolosa, A. verweyi, A. yongei*.
Tables and plates	15	*A. branchi, A. clathera, A. cytherea, A. divaricate, A. glauca, A. granulosa, A. hyacinthus, A. irregularis, A. lamarcki, A. latistella. A. macrostoma, A. mirablis, A. natalensis, A, pharaonis, A. willisae*
Bottlebrush	3	*A. forskali, A. horrida,* and *A. longicyathus*
Digitate	7	*A. arabensis, A. digitifera, A. gemmifera, A. humilis, A. monticulosa, A, ocellata, A. retusa*
Corymbose	13	*A. aculeus, A. anthoceris, A. appressa, A. cerealis, A. millepora, A. nana, A. nasuta, A. plantaginea, A. polystoma, A, samoensis, A. secale, A. tenuis, A. vermiculata*
Total	**64**	

4.3.3.1. Acropora encrusting

This cluster includes two species that are distinct from other *Acropora* species but sometimes difficult to distinguish. These two coral species, which were previously considered a subgenus of *Acropora* (*Isopora*), do not have axial corallites and they brood larvae. The two species are highly similar and differ in only two trait attributes: corallite spacing-crowded and asexual reproduction mode-fragmentation. While colonies can vary in their morphology from encrusting, solid plates, to short flattened branches they were most commonly observed as having encrusting morphologies and therefore this was the name given to the cluster. Even when these two species have more complex branching morphologies their surface texture and lack of axial corallites make them readily identifiable.

Since all *Acropora* begin life as encrusting juveniles, care was taken to distinguish between juveniles and encrusting *Acropora*. At the maximum size for juvenile

classification used in this study (2.5 cm diameter) most *Acropora* will have developed identifiable branching structures and can therefore be distinguished from *A. palifera* and *A. cuneata.*

4.3.3.2. Acropora staghorn

The cluster contains four common 'staghorn' species (*A. formosa, A. grandis, A. microphthalma, A. nobilis),* one uncommon species (*A. pulchra)* and one rare species (*A. copiosa*). These species varied only slightly in nine of the 26 traits examined: corallite spacing, daytime tissue projection, diel tissue expansion, egg colour, hardiness, morphological plasticity, polyp colour, reef attachment, and symbiont clade associations.

4.3.3.3. Acropora-bushy

This species cluster is characterized by bushy thicket-like colony morphologies. This large cluster contains eight common species (*A. brueggemanni, A. florida, A. hemprichii, A. loripes, A. robusta, A. squarrosa, A. verweyi,* and *A. yongei*), three sometimes common species (*A. abrotanoides, A. rosaria,* and *A. valida*), six uncommon species (*A. austera, A. inermis, A. pinguis, A. roseni, A, variablis,* and *A. variolosa*) and one rare species (*A. striata*). There were slight variations in 12 of the 26 traits examined including: egg colour, symbiont clade association, colony growth strategy, corallite spacing, maximum colony size, hardiness, asexual reproduction mode, polyp colour, daytime tissue projection, diel tissue expansion pattern, larval development (*A. brueggemanni* broods while the rest spawn), and morphological plasticity.

4.3.3.4. Acropora tables and plates

Tabular or plate-like morphologies encompass nine common species (*A. branchi, A. clathrata, A. cytherea, A. divaricate, A. glauca, A. granulosa, A. hyacinthus, A. lamarcki, A. pharaonis*), two sometimes common species (*A. irregularis, A. mirablis*), two uncommon species (*A. macrostoma* and *A. natalensis*), and two rare species (*A. latistella, A. willisae*). This group differed slightly in 11 of the 26 traits including: colony growth strategy, corallite spacing, daytime tissue projection, diel tissue projection pattern, egg colour, hardiness, maximum colony size, morphological plasticity, polyp colour spawning behaviour, and symbiont clade association.

4.3.3.5. Acropora-bottlebrush

The bottlebrush-like colony morphology encompasses only three species: one common (*A. longicyathus*) and two uncommon (*A. forskali* and *A. horrida*). These species differed slightly in nine of the 26 traits: corallite spacing, daytime tissue projection, diel tissue expansion pattern, hardiness, morphological plasticity, polyp colour, reef attachment, spawning behaviour and symbiont clade association.

4.3.3.6. Acropora-digitate

This cluster is characterized by finger-like colony morphologies and contains three common species (*A. arabensis, A. gemmifera, A. humilis*), three uncommon species (*A. digitifera, A. monticulosa, A. retusa*) and one rare species (*A. ocellata*). These species differed slightly in ten of 26 traits: colony growth morphology, corallite spacing, daytime tissue projection, diel tissue expansion pattern, hardiness, maximum colony size, morphological plasticity, polyp colour, spawning behaviour, and symbiont clade association.

4.3.3.7. Acropora-corymbose

This group is characterized by short fairly regular branches and contains six common species (*A. appressa, A. cerealis, A. millepora, A. nasuta, A. plantaginea, A. vermiculata*), two sometimes common species (*A. anthocercis, A. nana*) and five uncommon species (*A. aculeus, A. polystoma, A. samoenis, A. secale, A. tenuis*). The species differed in 12 traits: colony growth strategy, corallite spacing, daytime tissue projection, diel tissue expansion pattern, egg colour, hardiness, maximum colony size, morphological plasticity, polyp colour, reef attachment, spawning behaviour and symbiont clade association.

4.3.4. Montipora clusters

In contrast to *Acropora* it not possible to recognize a 'native' morphology in *Montipora* that can be used to identify species clusters. This is because *Montipora* is highly plastic, often exhibiting different growth forms within the same colony. For example, a colony may exhibit a submassive growth form with occasional foliose up-growths. In order to address the difficulty of identifying *Montipora* to species-level due to morphological plasticity, all *Montipora* species capable of exhibiting a particular colony morphology were included in the corresponding *Montipora* species cluster. In practice this meant that a species could belong to all five species clusters. This ensured the best possible chance of selecting the species that was actually present thereby resulting in the most realistic measures possible of species and trait abundance and diversity in downstream analysis.

The 27 species of *Montipora* present in Southwest Madagascar, their corresponding species cluster memberships, and global commonalities are summarized in Table 4.6. In total five species clusters, based on observed colony morphology, were used for *Montipora:* encrusting (all 27 species), submassive (22 species or 81 percent), laminar (15 species or 56 percent), branching/columnar (ten species or 37 percent), and foliose (two species or seven percent). Of the 27 *Montipora* species 16 (59 percent) are globally common, one (4 percent) is sometimes common, five (18.5 percent) uncommon, and five rare (18.5 percent).

All *Montipora* species present have scattered small corallites (27 species had corallites smaller than one millimetre while eight species could also have slightly bigger corallites (one to five millimetres) that divide via extratentacular budding to form colonies that are obligately attached to the reef. Corallite spacing is variable within *Montipora* species present ranging from crowded (six species), fairly crowded (seven species) to well spaced (18 species) and widely spaced (23 species). All species have short tentacles (less than ten millimetres long). Most *Montipora* species present have high plasticity (23 species) so exhibit many colony morphologies.

While all species can have tissue contracted during the day, 15 can sometimes expand their very short tentacles during the day. Only *Montipora venosa* can expand tissue beyond one millimetre during the day (between one and five millimetres). Most *Montipora* present have uniformly dull coloured polyps (23 species) or uniform bright polyps (21 species) while *Montipora informis* can also have corallites with bright centres.

All *Montipora* present are susceptible to bleaching but can recover quickly. None are resistant to bleaching or disease, all are susceptible to predation, and *M. lobulata* and *M. orientalis* are susceptible to disease. All *Montipora* species present associate only with clade C zooxanthellae with the exception of *M. aequituberculata,* which associates with both C and D.

All *Montipora* present are hermaphroditic spawners with symbionts present in their larvae. Spawning behaviour is via vigourous gamete ejection (although data was only available for one species) and eggs can be pink or tan. Three of the present *Montipora* species reproduce asexually via fragmentation: *M. aequituberculata*, *M. foliosa*, and *M. friablis*.

Table 4.6 *Montipora* species potentially present in Southwest Madagascar, their corresponding species cluster memberships, and global commonality.

Species	Encrusting	Submassive	Laminar	Branching/ Columnar	Foliose	Global commonality
M. hispida	1	1	1	1	0	Common
M. spongodes	1	1	1	1	0	Uncommon
M. verrucosa	1	1	1	1	0	Sometimes common
M. aequituberculata	1	1	1	0	1	Common
M. danae	1	1	1	0	0	Common
M. efflorescens	1	1	1	0	0	Common
M. effusa	1	1	1	0	0	Uncommon
M. friabilis	1	1	1	0	0	Uncommon
M. millepora	1	1	1	0	0	Common
M. mollis	1	1	1	0	0	Common
M. peltiformis	1	1	1	0	0	Uncommon
M. australiensis	1	1	0	1	0	Rare
M. calcarea	1	1	0	1	0	Rare
M. kellyi	1	1	0	1	0	Common
M. undata	1	1	0	1	0	Common
M. venosa	1	1	0	1	0	Uncommon
M. floweri	1	1	0	0	0	Rare
M. grisea	1	1	0	0	0	Common
M. informis	1	1	0	0	0	Common
M. lobulata	1	1	0	0	0	Rare
M. tuberculosa	1	1	0	0	0	Common
M. turgescens	1	1	0	0	0	Common
M. spumosa	1	0	1	1	0	Common
M. foliosa	1	0	1	0	1	Common
M. monasteriata	1	0	1	0	0	Common
M. orientalis	1	0	1	0	0	Rare
M. digitata	1	0	0	1	0	Common
Total	**27**	**22**	**15**	**10**	**2**	

4.3.5. Porites massive cluster

This species cluster consists of three common *Porites* species (*P. lobata, P. solida,* and *P. lutea*) that can all grow into massive bommie-like colonies but which are difficult to tell apart underwater without a handlens unless colonies are very well developed. These three species all have poor sediment shedding ability, small crowded, ceroid corallites that undergo extratentacular budding, determinate growth, short tentacles (less than ten millimetres long) and in Madagascar appear to show no tissue expansion by day. The species are resistant to bleaching but are susceptible to disease. The species do not recover quickly from bleaching and or disease and are not susceptible to predation. *Porites* species in this cluster reproduce sexually through gonochoric spawning with symbionts present in larvae. The colonies of species in this cluster can reach large maximum sizes of three metres (*P. lobata, P. lutea*) or five metres (*P. solida*) and all have low morphological plasticity and obligate reef attachment. These species associate only with clade C zoox. All three species can have uniform dull polyp colour, *P. lobata* and *P. lutea* can have uniform bright polyps, and *P. solida* can have bright polyp walls.

4.3.6. Cycloseris cluster

The membership, commonality, and trait variation in the cluster *Cycloseris* is summarized in Table 4.7. This cluster contains one common, two usually uncommon, one uncommon, and one rare *Cycloseris* species, which all have very high trait similarity and only differed in seven out of 136 attributes (see Table 4.7).

Table 4.7 *Cycloseris* species potentially present in SW Madagascar, their global commonality, and trait dissimilarity. *Cycloseris* has very high trait similarity and only differ in seven of 136 trait attributes.

Species	**Commonality**	Daytime tissue projection -5 to 20 mm	Diel tissue expansion pattern -tentacles extended by day	Maximum colony size -10cm max	Maximum colony size -30 cm max	Polyp colour -center bright	Polyp colour -wall bright	Tentacle length -10 to 20 mm
C. costulata	rare			1			1	
C. curvata	uncommon	1	1	1				
C. erosa	rare	1	1	1				
C. cyclolites	common	1	1	1				1
C. patelliformis	usually uncommon			1		1		
C. vaughani	rare			1		1		
C. tenuis	rare		1	1				
C. somervillei	usually uncommon				1			

*4.3.7. **Fungia cluster***

The *Fungia* species cluster contains all of the 15 *Fungia* species known to occur in Ecoregion 16 including ten common species (*F. concinna, F. corona*, *F. danai, F. fungites, F. horrida, F. klunzingeri, F. paumotensis, F. repanda, F. scutaria*) and six uncommon species (*F. moluccensis, F. puishani, F. scabra, F. scruposa* and *F. seychellensis, F. granulosa).*

All species are obligate freeliving species, with determinate growth, a maximum colony size of 30 cm, and low morphological plasticity. All *Fungia* species present can have tentacle lengths of ten to 20 mm and five species can have tentacles lengths shorter than ten mm. Tentacles can be expanded by day in five of the present *Fungia*

species. All species are gonochoric spawners without symbionts present in larvae. *Fungia fungites* can also reproduce by brooding larvae.

None of the present *Fungia* species were resistant to bleaching, and half were susceptible to bleaching but could also recover quickly from bleaching or disease while the other half were not susceptible to bleaching but also did not recover quickly from bleaching and disease. No species were resistant or susceptible to disease. As defined by Veron, all *Fungia* present had widely spaced corallites, and calice/valley widths of less than 15 mm wide.

F. puishani, *F. scruposa*, *F. moluccensis* and *F. seychellensis* (all uncommon) could be colonial (have multiple mouths) with peripheral mouths (scattered corallite form) budding outside the axial furrow via extratentacular budding. Two of these corals also had polystomatous axial furrows that formed via intratentacular budding (*F. moluccensis* and *F. seychellensis)* resulting in submeandroid corallites. All other corals in this group were considered non-colonial, plocoid corallites that did not undergo intra- or extratentacular budding.

4.3.8. Summary

In this section the species clusters and method by which they were replaced by species in the analysis were focussed upon, because while species present in clusters are highly similar in terms of traits, there are some differences between species. While all species clusters were evident as emergent groups (detailed in Chapter Five) and exhibit high levels of self-similarity, they are not necessarily considered as functionally equivalent here, rather they are used as a means for handling species-identification uncertainty.

4.4. Database

4.4.1. Database Structure

In order keep the data clearly organized and accessible a relational database was created using Microsoft Access. The database objects, data elements and the relationships between the objects are visualized in Figure 4.12. All real world objects are represented in the flow diagram as separate boxes and in the actual database as a table. All database elements associated with an object are listed within the object box and are table columns in the actual database. The real world objects represented in the database are summarized in Table 4.8. The data elements associated with the data objects are described in Table 4.9.

Table 4.8 Description of each object in the comprehensive relational database for this study.

Object name	**Object description**
Points	The three points randomly scattered on each image by CPCe
Point occupants	The coral species, coral species cluster, other reef organism or substrate type that lies under a point
Images	The photoquadrat images
Transects	Combinations of sequential images at each reef site
Sites	Reef site (i.e. A1)
Coral Traits	*Scleractinian* coral traits (i.e. calice width, growth rate)
I	Intersecting object to manage 'many to many' relationship that occurs between point occupant and trait
II	Intersecting object to manage 'many to many' relationship that occurs between point occupant and trait

Table 4.9 Description of each data element in the comprehensive relational database for this study.

Data element name	**Data element description**
Point name	The unique name assigned to each identification point scattered on the photoquadrat images by CPCe (i.e. A01_20091127123134_NBR_06.4.jpgA
Point code	The unique code assigned in the CPCe code file to identify each coral species, coral species cluster, other reef organism, or substrate type (i.e. BT = brown turf algae)
Point type	General substrate type (hard coral, soft coral, sponges, algae, other, substrate, unknown)
Genus code	A code referring to the genera that coral species belongs to (i.e. *Acropora*)
Species name	The coral species name (i.e. *Acropora robusta*)

Data element name	**Data element description**
Species cluster	The coral species cluster that a coral species belongs to in the case were a number of species are difficult to identify based on photos alone (i.e. *Acropora* bushy)
Weighting	The weighting given to a coral species in a cluster that determines its likelihood of being selected as representative of the cluster in the calculation of functional diversity metrics. The weighting is based on the commonality cited in Veron (2000) i.e. rare, uncommon, common
Trait name	The name of a coral trait (i.e. branching: 2D dominant)
Trait category	The name of the category to which a trait can belong (i.e. branching)
Trait description	Description of a coral trait (i.e. 2 dimensional branching structure)
Trait publication reference	The source of the trait data (i.e. Veron, 2000)
Image Name	The unique name of a photoquadrat image (i.e. A01_20091127123134_NBR_06.4)
Image depth	The depth at which the photoquadrat image was taken (i.e. 6.4 m)
Longitude	Longitude for the location at which the image was taken in decimal degrees (i.e. 43.26645)
Latitude	Latitude for the location at which the image was taken in decimal degrees (i.e. -21.873606)
Transect ID name	The name of a particular transect on a particular reef site (i.e. A1.T1)
Depth category	The depth category to which an image or transect belongs (i.e. 5-10 m).
Site code	The site code for a reef site (i.e. A1)
Site name	The name for a reef site (i.e. No Bad Reef)
Region name	The name of the study region in which a reef site is found (i.e. Velondriake)
Geomorphology	The geomorphology of a particular reef site: patch reef, fringing reef, or spur and groove system
Reef type	The reef type of a particular site (i.e. M.1; see Ch. 4)
Number of huts	The number of Vezo fishing huts within a 10 km radius of the reef site as counted from satellite images.
Distance to river	The distance in km between a reef site and the nearest river mouth as measured from satellite images.
Average annual SST	The average annual sea surface temperature (SST) in Celsius for a reef site calculated using NOAA satellite images.
Fetch	The distance in km seaward from the reef site to the nearest obstacle.

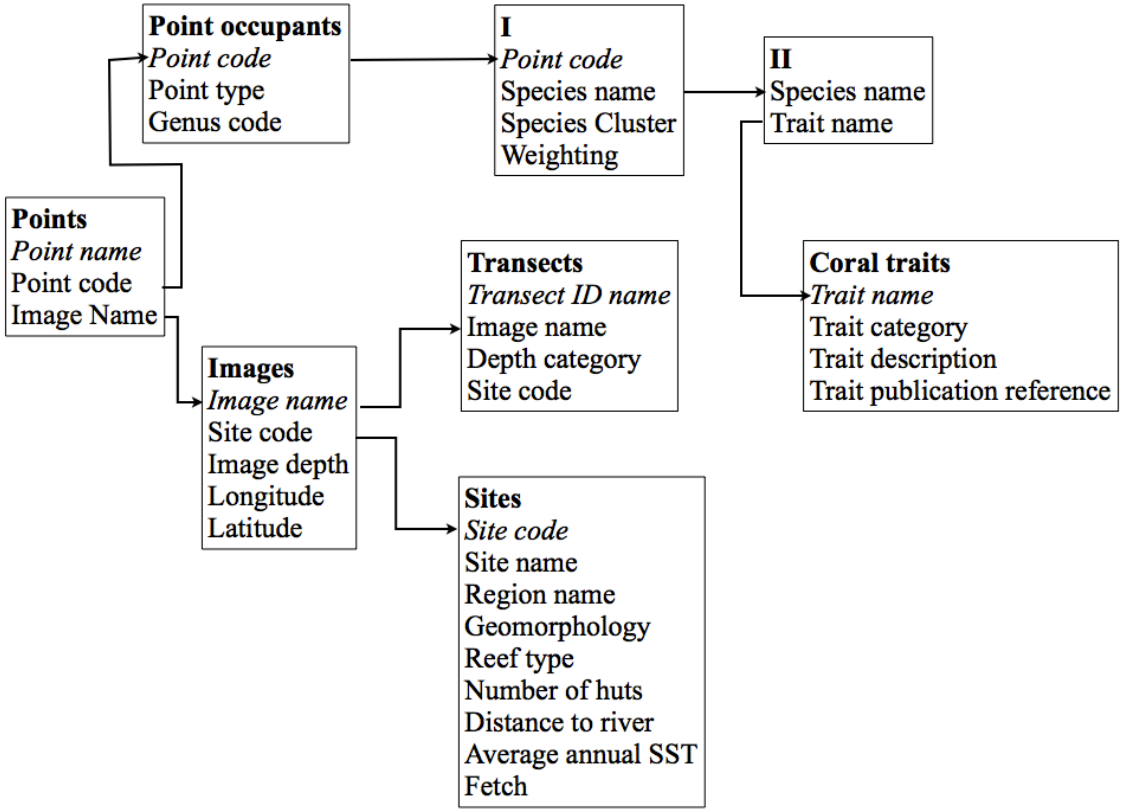


Figure 4.12 Overview of comprehensive relational database constructed for the study. Each box represents a real world object and the name of that object is indicated by the bold text. The data elements are listed in non-bold text and the primary keys are indicated by italic text. The arrows show the relationships between the objects. The many-to-many relationship that exists between point occupants and coral traits is managed by the intersecting objects I and II.

4.5. Sampling area and effort

The cost of underwater reef surveys is high, especially in remote areas like Madagascar, where poor road infrastructure makes petrol delivery for boats exceptionally expensive. Because of the high costs involved, in combination with the logistical and safety challenges of conducting reef surveys in a remote region, it was essential to streamline data collection and collect as much data as possible during each 25-75 minute dive.

The amount of total dive time spent allocated to each reef site was directly related to the depth of the reef (air consumption rates increase with depth) and the strength of the currents present at each site (strong currents require increased physical effort which increases air consumption rates). The amount of total dive time allocated to each reef site determined how many photoquadrat images could be taken and how much area could be sampled.

It is common to predetermine the number of photoquadrat images and transects to be conducted at each reef site and depth. Unfortunately, this was not a practical approach for surveying the reef sites in Southwest Madagascar since documentation for most of the reef sites were either poor or absent. Information about reef type, depth, and size were often not known prior to surveying. Therefore the goal became to gather as much data as possible and to then construct a sampling design based on the data that could be collected. This involved determining: 1.) the depth zones to compare between sites, 2.) the level of total sampling area (i.e. no. of images) at which to compare reef sites in each depth zone and 3.) the level of sampling effort (per image) at which to compare the the sites. The methodology used for making these decisions is laid out in the following three sections.

4.5.1. Selection of depth ranges

Because coral species compositions on reefs change with depth, resulting in zonation, only similar depth zones can be compared between reefs. Therefore the entire data set containing 6853 images, each with three point identifications, were divided into depth ranges. Prior to field sampling the following depth categories were selected: 0-2, 2-5, 5-10, 10-15, 15-25, and 25-35 m.

Most reef sites shallow enough to allow for data collection at 0-2 m were located in the Bay of Ranobe and were dominated by macro algae at this depth. Since coral coverage was so low at this depth range these samples were dropped from the analysis. Also because air consumption and therefore sampling time penalty increases by depth only two sites could be surveyed at depths below 26 m and therefore this depth range was also excluded from the analysis, leaving four depth categories in total (2-5, 5-10, 10-15, 15-26 m).

To examine whether these depth categories were capturing the zonation pattern of the major space occupying corals species, distributions were plotted by depth. The depth recorded for each observation point was accurate to 0.1 m; in the interest of visual representation this was rounded to the nearest metre. The coral species frequency was then calculated for each metre interval and plotted (Figure 4.13).

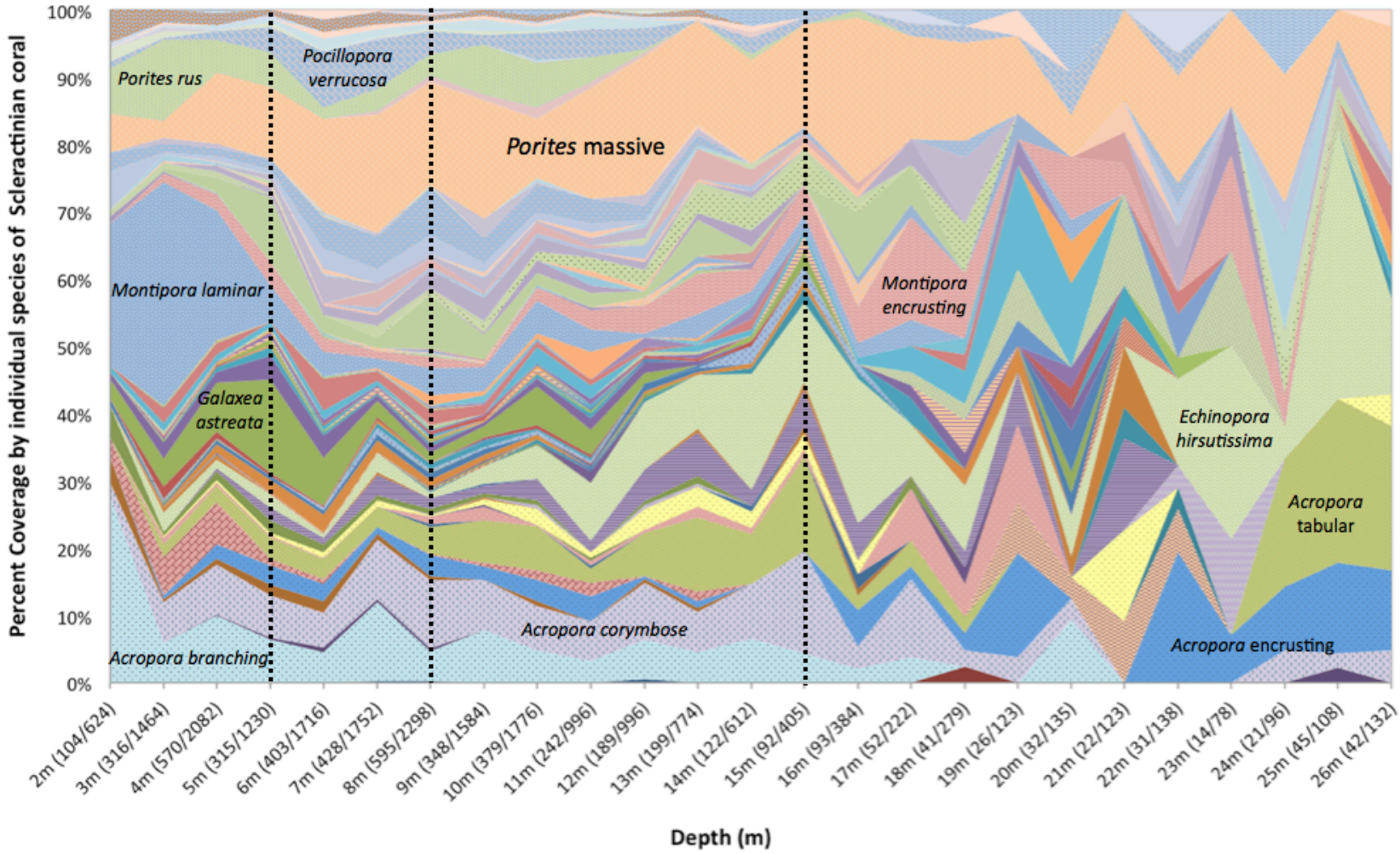

Percent Coverage by individual species of Scleractinian coral
100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
Porites rus
Pocillopora verrucosa
Porites massive
Montipora laminar
Montipora encrusting
Galaxea astreata
Echinopora hirsutissima
Acropora tabular
Acropora corymbose
Acropora branching
Acropora encrusting
2m (104/624)
3m (316/1464)
4m (570/2082)
5m (315/1230)
6m (403/1716)
7m (428/1752)
8m (595/2298)
9m (348/1584)
10m (379/1776)
11m (242/996)
12m (189/996)
13m (199/774)
14m (122/612)
15m (92/405)
16m (93/384)
17m (52/222)
18m (41/279)
19m (26/123)
20m (32/135)
21m (22/123)
22m (31/138)
23m (14/78)
24m (21/96)
25m (45/108)
26m (42/132)
Depth (m)

Figure 4.13 Percent coverage by coral species and depth (rounded to the nearest metre). The x-axis is labelled by depth and in parentheses the number of coral points and total points for the depth is given. The depth zones that were found to best reflect the zonation patterns of the coral composition were 2-5 m, 5-8 m, 8-15 m, and 15-26 m (indicated in figure by vertical black dotted lines).

Laminar *Montipora* spp.*,* branching *Acropora* spp. and *Porites rus* were major space occupiers between two to five metres but they decrease in abundance at depths greater than five metres. The depth range two to five metres is therefore capturing this zonation pattern and was used in further analysis.

Another zone occurs from five to eight metres as the dominance of laminar *Montipora* spp. gives way to *Porites* massive spp. and species diversity generally increases. At eight to 15 m the presence of tabular *Acropora* spp. and *Echinopora hirussitima* increases while branching *Acropora* spp., corymbose *Acropora* spp. and *Porties* massive spp. continue as prominent features. Below 15 m another zone occurs dominated by encrusting *Montipora* spp., *Echinopora hirssutisima*, tabular *Acropora* spp., *Porites* massive spp., *Acropora* encrusting spp., *Pachyseris speciosa*, and *Favia speciosa.*

Based on the above observation the original depth categories were adjusted to: 2-5, 5-8, 8-15, and 15-26 m. The number of photoquadrat images available for each depth range is summarized in Table 4.10. The table also summarizes the total survey area for each depth category (0.558 m^2 x number of images available), the number of reef sites for each depth category belonging to each geomorphology category (light green), and study region (light yellow).

Table 4.10 Summary table of number of images, area (no. images x 0.558 m^2), and the number of reef sites for each depth category belonging to each geomorphology category (light green), and study region (light yellow). NB Not all data was used in subsequent analyses and this is detailed in the following sections.

Depth Category (m)	Number of images	Area surveyed (m^2)	Patch reefs	Fringing reefs	Spur and grove systems	Velondriake	Ranobe	Tulear
2-5	1544	861.5	10	19	5	11	13	10
5-8	1755	979.3	16	20	9	20	14	11
8-15	2677	1493.8	18	14	11	24	8	11
15-26	637	355.5	9	2	11	11	8	3
Total	6613	3690.1	62	62	36	70	52	38

4.5.2. Selection of sampling area at which to compare reef sites

The quantity of images taken at each reef site and depth varied (see Appendix Four), therefore direct comparisons of species richness and abundance was not appropriate. Reef sites compared for a particular depth zone were all compared at a set sampling area (number of photos) determined using Species Area Curves. Whilst this meant that some data was discarded it was important that reef sites were compared at similar levels of sampling effort.

In order to aid the selection of the most appropriate sampling area at which to compare the sites for each depth range, Species Accumulation Curves (hereafter SACs) were created. SACs were coded in **R** making use of the *rarefaction* method of the **specaccum( )** function available in the package **vegan**. This method finds the expected species richness and its standard deviation through sampling individuals instead of sites. The annotated **R** script for the SACs is available in Digital Supplement 1.3. Species clusters (i.e. *Acropora* branching) were considered as one 'species' and all non-coral point codes were combined into an 'other' category which were also counted as one species.

The level of sampling effort at which to compare sites was determined based on the steepness of the SAC. The level of sampling at which sites were compared is shown as red vertical hashed line in the SACs (Figure 4.14 to Figure 4.17) and is also summarized in Table 4.11

Sites with insufficient data for a depth range were excluded while for sites that had surplus data only the data up to the cut-off point was used. While this method resulted in some unused data it was essential to ensuring that sites were compared at the same sampling effort. The number of sites included for each depth range and the sampling effort at which they were compared are summarized in the following table.

Table 4.11 Summary of no. of sites and level of sampling effort at which the sites were compared.

Depth range (m)	**No. of sites included**	**Sampling effort (no. of points/images) at which sites are compared**	**Survey area (m^2) at which sites are compared**
2-5	21	93/31	17.30
5-8	21	102/34	19.97
8-15	34	96/32	17.86
15-26	17	54/18	10.04

4.5.2.1. 2-5 m depth range

Between two to five metres depth, 21 sites had sufficient images (≥ 31 images or 93 points) for subsequent analyses (Table 4.12). The 21 sites are evenly distributed between the three study regions and consist mostly of fringing reefs (n = 12), and shallow patch reefs (n = 8). The sites are well distributed along gradients of fishing intensity, sedimentation, and fetch.

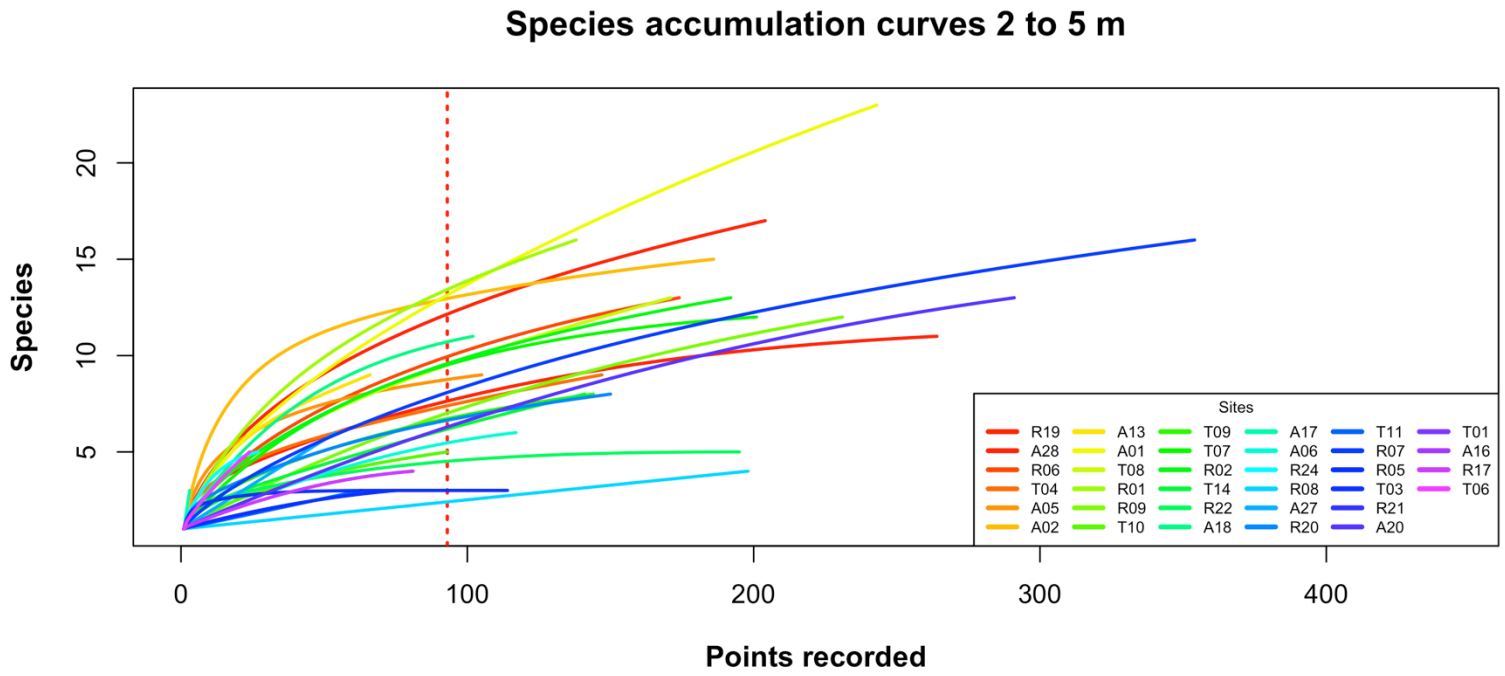


Figure 4.14 Species accumulation curves for the 34 sites with points available at two to five metres depth. Any non-coral points are grouped together as one 'species' while species clusters (i.e. *Acropora* branching) are also counted as one 'species'. The vertical dotted line indicates the sampling effort at which sites are compared (93 points). Sites with insufficient data (<93 points) were excluded from analysis. While for site with excessive data (>93 points) only the first 93 points in the sample were used. In total 21 sites had a sufficient no. of data points and coral cover and could therefore be included in downstream analysis (see Table 5.6).

Table 4.12 Table summarizing environmental variables and reef typology for the 21 reefs compared at the 2 to 5 m depth range. The first 93 points for each reef site were used in the subsequent comparative analysis. Two reef sites (site R07 and A20) had a sufficient number of points but no coral cover in these first 93 points and were therefore discarded from the analysis and are not listed here.

Site	**Total Points available** (no. image x 3 pts each)	**Geomorphology**	**Region**	**Reef Type**	**Fishing intensity** (No. of huts within a 10 km radius)	**Sedimentation** (km to nearest river mouth)	**Fetch** (km to nearest seaward facing object)
A01	243	Fringing	Velondriake	MMR.1	690	46.09	0.29
A02	186	Spur and Groove	Velondriake	SG.2	510	49.46	800
A05	105	Patch	Velondriake	MMR.1	500	58.92	800
A06	117	Patch	Velondriake	MMR.1	768	61.59	800
A18	102	Patch	Velondriake	MMR.3	634	68.9	3.43
A28	204	Fringing	Velondriake	CW	730	75.3	800
R01	138	Fringing	Ranobe	MMR.3	920	15	4.09
R02	192	Fringing	Ranobe	MMR.4	920	9.48	2.96
R06	174	Fringing	Ranobe	RF.1	1170	11.54	800
R08	198	Fringing	Ranobe	RF.1	1170	13.54	2.8
R09	231	Fringing	Ranobe	RF.1	1170	14.16	2.9
R19	264	Patch	Ranobe	MMR.4	510	18.3	1.6
R20	150	Patch	Ranobe	MMR.4	590	17.2	2.18
R22	195	Patch	Ranobe	MMR.4	540	15.4	0.1
T03	114	Fringing	Tulear	RF.2	2385	7.43	0.2
T04	147	Fringing	Tulear	RF.2	2385	7.9	0.23
T07	201	Patch	Tulear	MMR.4	1792	13.11	0.3
T08	171	Patch	Tulear	MMR.3	477	11.69	0.4
T09	144	Fringing	Tulear	MMR.3	927	10.3	4.44
T10	93	Fringing	Tulear	MMR.3	927	8.7	4.3
T14	141	Fringing	Tulear	MR.2	917	3.72	800

4.5.2.2. 5-8 m depth range

At the 5-8 m depth range, 21 reef sites had sufficient images (≥ 34 images or 102 points) available to be included in subsequent analyses (see Table 4.13). These were located mainly in Velondriake (n = 13), Tulear (n = 6) with only two sites in Ranobe. Sites were fairly evenly distributed between geomorphological type (five patch reefs, six spur and groove systems, and ten fringing reefs), fishing intensity (no. of huts within a ten kilometre radius), sedimentation stress (distance to river), and fetch (distance to nearest object seaward).

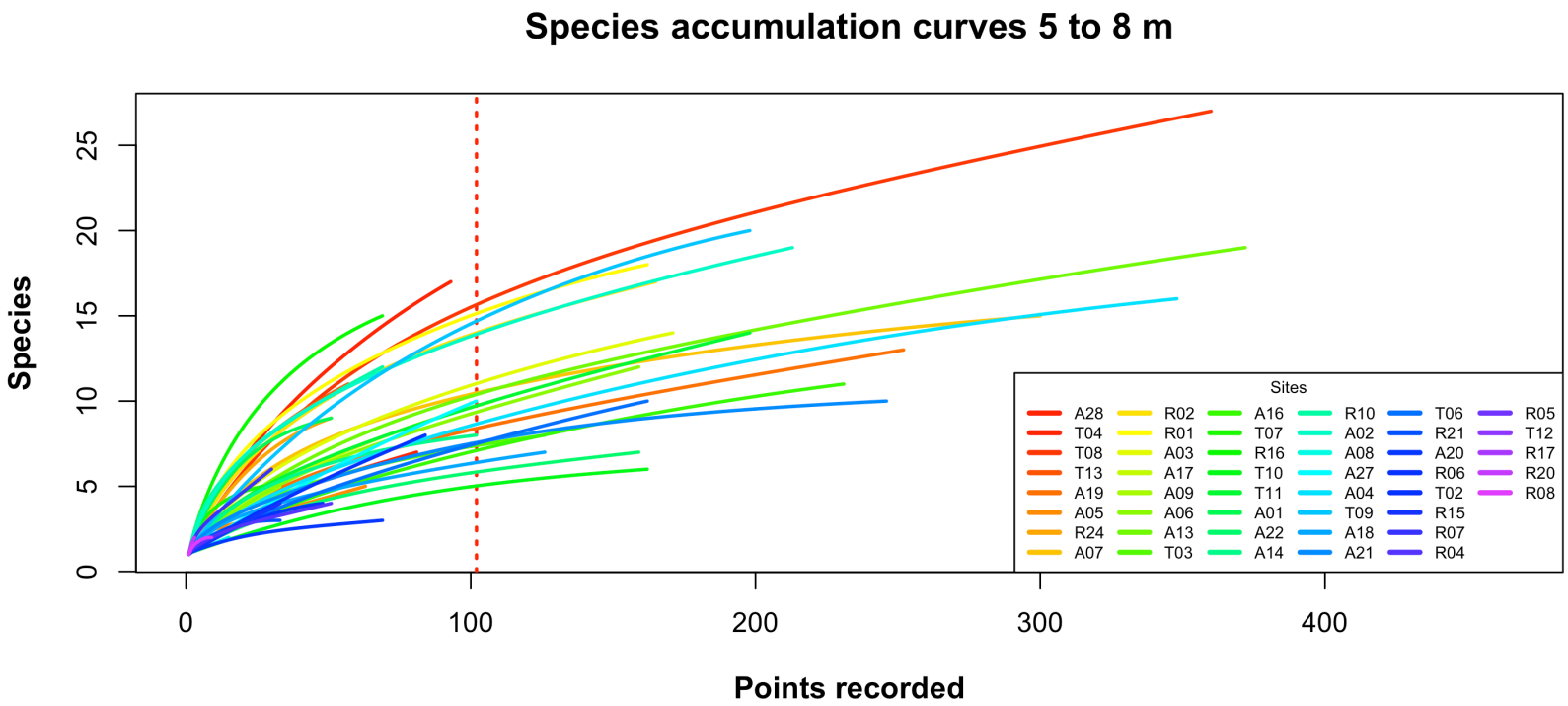


Figure 4.15 Species accumulation curves for the 45 sites with points available at five to eight metres depth. Any non-coral points are grouped together as one 'species' while species clusters (i.e. *Acropora* branching) are also counted as one 'species'. The vertical dotted line indicates the sampling effort at which sites are compared (102 points). Sites with insufficient data (<102 points) were excluded from analysis. While for site with excessive data (>102 points) only the first 102 points in the sample were used. In total 21 reef sites had sufficient data and coral cover and could therefore be included in downstream analysis (Table 5.7).

Table 4.13 Table summarizing environmental variables and reef typology for the 21 reefs compared at the five to eight metre depth range. The first 102 points for each reef site were used in the subsequent comparative analysis. One reef sites (A21) had a sufficient number of points but no coral cover in the first 102 points and was therefore not included in downstream analysis.

Site	**Total Points available** (no. image x 3 pts each)	**Geomorphology**	**Region**	**Reef Type**	**Fishing intensity** (No. of huts within a 10 km radius)	**Sedimentation** (km to nearest river mouth)	**Fetch** (km to nearest seaward facing object)
A02	213	Spur and Groove	Velondriake	SG.2	510	49.46	800
A03	171	Fringing	Velondriake	M.2	638	55.17	800
A04	348	Spur and Groove	Velondriake	SG.6	380	60.37	800
A06	159	Patch	Velondriake	MMR.1	768	61.59	800
A07	300	Patch	Velondriake	MMR.1	810	62.99	0.4
A13	372	Spur and Groove	Velondriake	SG.3	560	72.3	800
A14	102	Fringing	Velondriake	SG.3	560	70.32	800
A16	231	Fringing	Velondriake	M.4	634	67.65	3.4
A17	108	Fringing	Velondriake	M.4	634	68.5	800
A18	126	Patch	Velondriake	MMR.3	634	68.9	3.43
A19	252	Patch	Velondriake	M.1	870	70.02	3.4
A22	159	Spur and Groove	Velondriake	SG.2	460	74.71	800
A27	102	Spur and Groove	Velondriake	SG.4	710	75.46	800
R01	162	Fringing	Ranobe	MMR.3	920	15	4.09
R02	165	Fringing	Ranobe	MMR.4	920	9.48	2.96
T03	126	Fringing	Tulear	RF.2	2385	7.43	0.2
T06	162	Spur and Groove	Tulear	SG.3	1525	15.6	800
T08	360	Patch	Tulear	MMR.3	477	11.69	0.4
T09	198	Fringing	Tulear	MMR.3	927	10.3	4.44
T10	162	Fringing	Tulear	MMR.3	927	8.7	4.3
T11	198	Fringing	Tulear	MMR.3	927	8.9	800

4.5.2.3. 8-15 m depth range

At the 8-15 m depth range 34 reef sites had sufficient images (≥ 32 images or 96 points) for analyses. These consisted of patch reefs (n = 14), spur and groove systems (n = 11), and fringing reefs (n = 9). The sites were located in Velondriake (n = 19), Tulear (n = 8), and Ranobe (n = 7). Sites were spaced evenly along a gradient of fishing intensity (no. of huts within a ten km radius), and sedimentation stress (distance to river). Most sites (24 of 34) with reef surface at this depth were located outside the barrier reef and not sheltered.

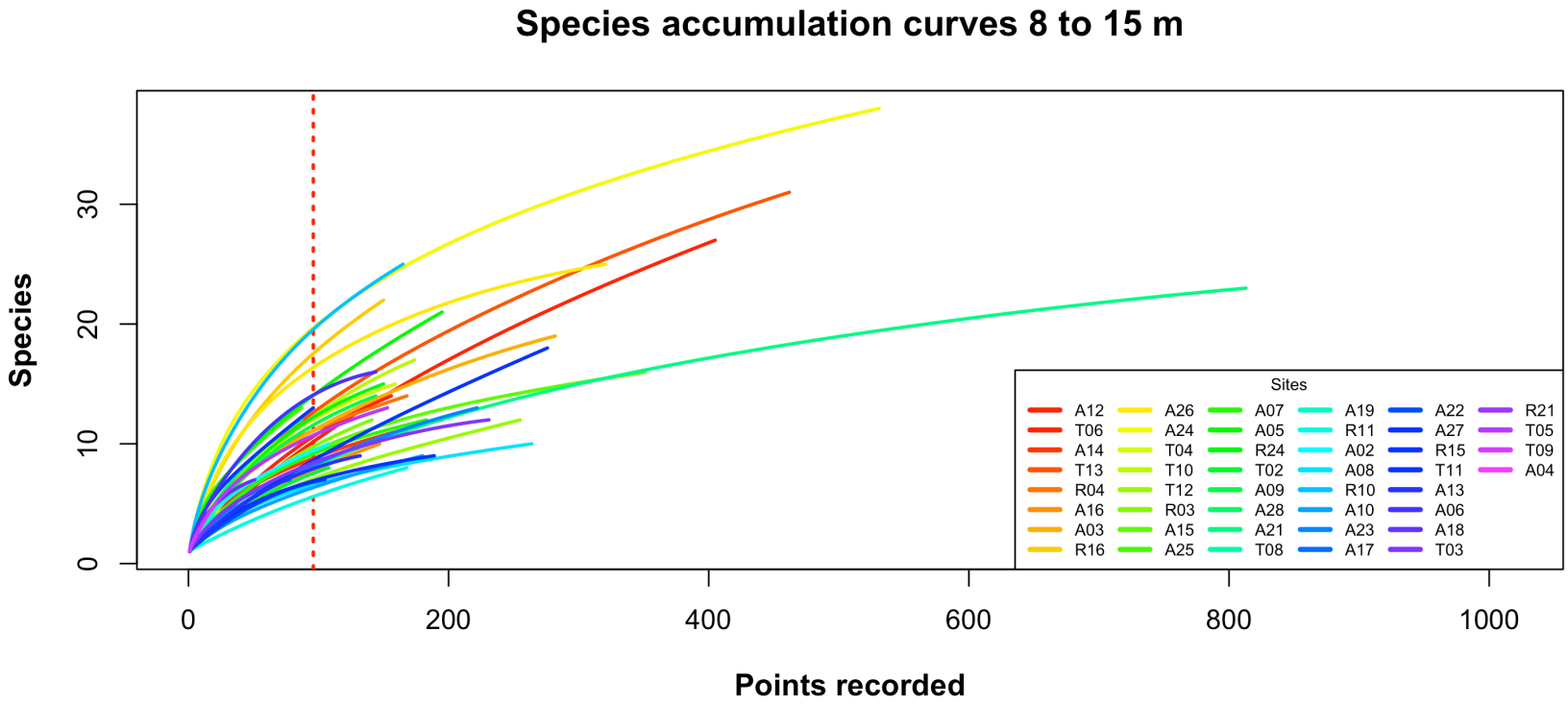


Figure 4.16 Species accumulation curves for the 44 sites sites with points available at eight to 15 metres depth. Any non-coral points are grouped together as one 'species' while species clusters (i.e. *Acropora* branching) are also counted as one 'species'. The vertical dotted line indicates the sampling effort at which sites are compared (96 points). Sites with insufficient data (<96 points) were excluded from analysis. While for site with excessive data (>96 points) only the first 96 points in the sample were used. In total 34 sites had sufficient data and coral cover to be included in downstream analysis.

Table 4.14 Table summarizing environmental variables and reef typology for the 21 reefs compared for the 8 to 15 m depth range. The first 96 points for each reef site were used in the subsequent comparative analysis. Reef sites with a sufficient number of points but without any coral cover in the first 96 points were discarded from the analysis and are not listed here (site T03).

Site	**Total Points available** (no. image x 3 pts each)	**Geomorphology**	**Region**	**Reef Type**	**Fishing intensity** (No. of huts within a 10 km radius)	**Sedimentation** (km to nearest river mouth)	**Fetch** (km to nearest seaward facing object)
A03	282	Fringing	Velondriake	M.2	638	55.17	800
A09	144	Fringing	Velondriake	CW	600	67.39	800
A10	180	Fringing	Velondriake	M.2	608	70.2	800
A14	195	Fringing	Velondriake	SG.3	560	70.32	800
A16	147	Fringing	Velondriake	M.4	634	67.65	3.4
T04	159	Fringing	Tulear	RF.2	2385	7.9	0.23
T10	174	Fringing	Tulear	MMR.3	927	8.7	4.3
T11	96	Fringing	Tulear	MMR.3	927	8.9	800
T12	255	Fringing	Tulear	M.3	927	9.7	800
A05	195	Patch	Velondriake	MMR.1	500	58.92	800
A06	144	Patch	Velondriake	MMR.1	768	61.59	800
A07	183	Patch	Velondriake	MMR.1	810	62.99	0.4
A08	264	Patch	Velondriake	MMR.1	810	63.1	0.33
A12	405	Patch	Velondriake	M.2	560	72	800
A15	351	Patch	Velondriake	M.2	634	72.6	800
A21	813	Patch	Velondriake	MMR.3	669	80	0.55
A23	222	Patch	Velondriake	MR.1	710	75.02	2.7
A24	531	Patch	Velondriake	MR.1	710	75.9	0.6
A26	321	Patch	Velondriake	MMR.1	710	79.24	0.78
R04	168	Patch	Ranobe	MR.1	920	10	800
R10	165	Patch	Ranobe	MR.3	1170	17.85	1.8
R16	150	Patch	Ranobe	M.5	470	17.8	800
T13	462	Patch	Tulear	M.3	1127	7.39	800
A02	108	Spur and Groove	Velondriake	SG.2	510	49.46	800
A13	132	Spur and Groove	Velondriake	SG.3	560	72.3	800
A22	105	Spur and Groove	Velondriake	SG.2	460	74.71	800
A27	189	Spur and Groove	Velondriake	SG.4	710	75.46	800

Site	**Total Points available** (no. image x 3 pts each)	**Geomorphology**	**Region**	**Reef Type**	**Fishing intensity** (No. of huts within a 10 km radius)	**Sedimentation** (km to nearest river mouth)	**Fetch** (km to nearest seaward facing object)
R03	141	Spur and Groove	Ranobe	SG.2	770	14.39	800
R11	168	Spur and Groove	Ranobe	SG.2	920	17.64	800
R15	276	Spur and Groove	Ranobe	SG.2	440	20	800
R24	150	Spur and Groove	Ranobe	SG.5	540	12.2	800
T02	108	Spur and Groove	Tulear	SG.2	2385	7.15	800
T05	153	Spur and Groove	Tulear	SG.1	2385	10	800
T06	156	Spur and Groove	Tulear	SG.3	1525	15.6	800

4.5.2.4. 15-26 m depth range

Seventeen sites located at the 15-26 metre depth range had sufficient images (≥ 18 images or 54 points) and coral cover for subsequent analyses They were mostly located in Velondriake (n = 10) but also in Ranobe (n = 4) and Tulear (n = 3). Sites consisted patch reefs (n = 8), spur and groove systems (n = 7) and deep fringing reefs (n = 2). Most of the reef sites (13 of 17) at this depth were either located outside the barrier reef or otherwise not protected.

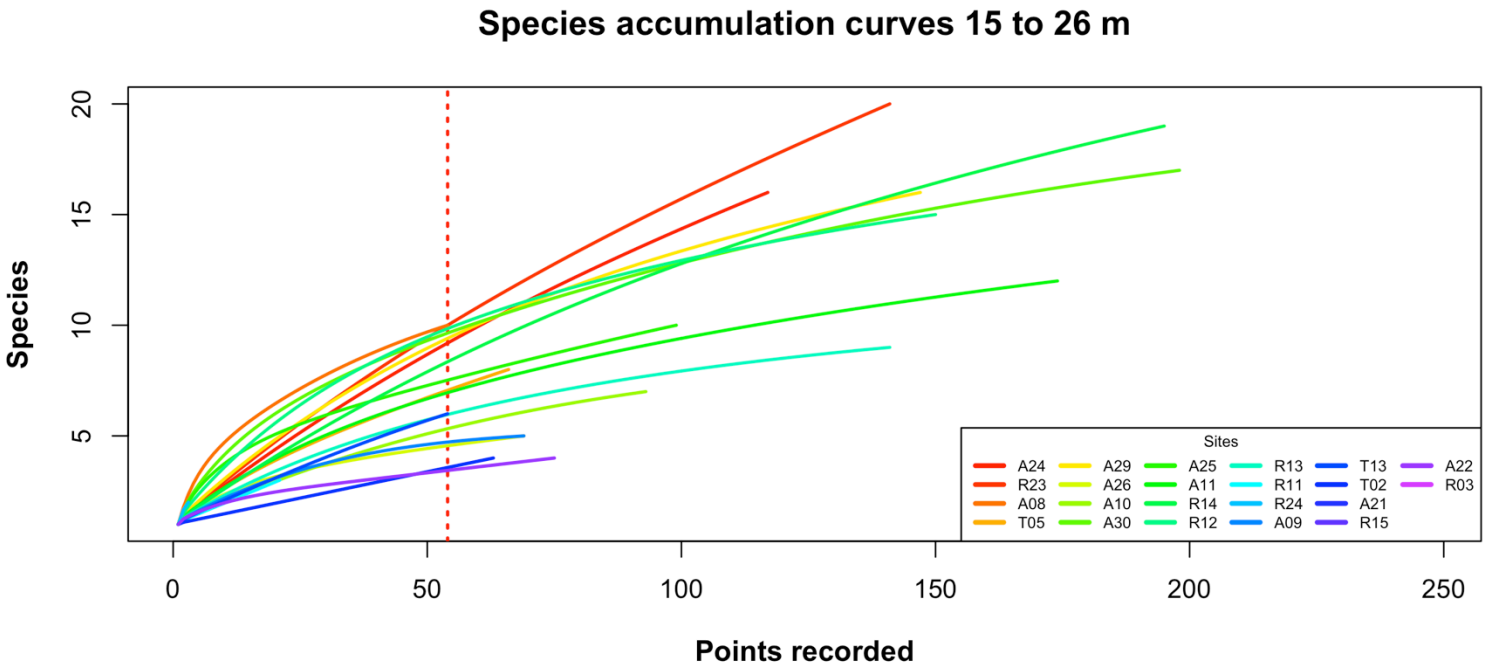


Figure 4.17 Species accumulation curves for the 22 sites with points available at 15 to 26 metres depth. Any non-coral points are grouped together as one 'species' while species clusters (i.e. *Acropora* branching) are also counted as one 'species'. The vertical dotted line indicates the sampling effort at which sites are compared (54 points). Site with insufficient data (< 54 points) were excluded from analysis. While for site with excessive data (> 54 points) only the first 54 points in the sample were used. In total, 17 sites had sufficient data and coral cover to be included in downstream analysis (see Table 5.9).

Table 4.15 Table summarizing environmental variables and reef typology for the 17 reefs compared at the 15 to 26 m depth range. The first 54 points for each reef site were used in the subsequent comparative analysis. All reef sites with a sufficient number of points also had coral cover in the first 54 points and therefore all sites were included in subsequent analyses.

Site	**Total Points available** (no. image x 3 pts each)	**Geomorphology**	**Region**	**Reef Type**	**Fishing intensity** (No. of huts within a 10 km radius)	**Sedimentation** (km to nearest river mouth)	**Fetch** (km to nearest seaward facing object)
A09	69	Fringing	Velondriake	CW	600	67.39	800
A10	93	Fringing	Velondriake	M.2	608	70.2	800
A08	54	Patch	Velondriake	MMR.1	810	63.1	0.33
A11	174	Patch	Velondriake	M.2	466	71.36	800
A24	117	Patch	Velondriake	MR.1	710	75.9	0.6
A25	99	Patch	Velondriake	MR.1	710	75.9	0.65
A26	69	Patch	Velondriake	MMR.1	710	79.24	0.78
A29	147	Patch	Velondriake	M.2	573	79.02	800
A30	198	Patch	Velondriake	M.2	120	84.3	800
T13	54	Patch	Tulear	M.3	1127	7.39	800
A22	75	Spur and Groove	Velondriake	SG.2	460	74.71	800
R12	150	Spur and Groove	Ranobe	SG.1	720	19.73	800
R13	141	Spur and Groove	Ranobe	SG.1	470	20.05	800
R14	195	Spur and Groove	Ranobe	SG.1	390	18.65	800
R23	141	Spur and Groove	Ranobe	SG.1	540	16.1	800
T02	63	Spur and Groove	Tulear	SG.2	2385	7.15	800
T05	66	Spur and Groove	Tulear	SG.1	2385	10	800

4.5.3. Sampling effort per image

Field methods proved efficient, yielding 6,853 photoquadrat images and an additional 2,000 descriptive photos of the reef sites. Due to the time required to visually analyse this large amount of images it was important to determine the quantity of images, and identification points per image, that would result in the best species richness estimate for a given image analysis effort.

A sampling-effort analysis was conducted on two reef sites, A07 and R14 to determine how the species richness recorded for the sites varied with the number of points identified for each image. Two reefs were selected for analysis based on a previous pilot study in which Species Area Curves (SACs) were calculated for 38 reef sites using three points for each image. It was clear that some of the SACs had nearly reached an asymptote while others were almost linear in shape. The reef site A07 is representative of the SACs that were nearing their asymptote while R14 is representative of reef sites that had a nearly linear SAC. Information regarding the two sites is summarized in Table 4.16.

Table 4.16 Summary of sampling effort, coral coverage, coral species richness and environmental conditions at site A07 and R14. These two sites were reanalysed to test how increasing the number of sampling points per image from three to six impacted on the overall species richness recorded and also on the shape of the species accumulation curve.

Reef Site	**A07**	**R14**
Photoquadrat Images	153	65
Points	918	390
Coral Points	185	54
% Coral cover	20.1%	13.8%
Coral Species Richness (no. of coral species)	27	22
Reef type	MMR1	SG1
Geomorphology	Patch reef	Spur and groove
Huts within a 10km radius	810	390
Fetch (km seaward to nearest obstructing object)	0.4	800
Sedimentation (km from nearest river)	62.99	18.65

The reanalysis involved adding three extra random sampling points to each image for a total of six points per image. Species accumulation curves were then created by randomly sampling the images without replacement and in turn randomly sampling

from the points available on each image. In order to create a smoothed curve n = 1000 samples were taken.

It is clear from the species accumulation curves for both A07 (Figure 4.18) and R14 (Figure 4.19) that allocating fewer points to more images rather than more points to fewer images for a set sampling effort (points sampled) resulted in a higher overall number of species recorded. This is evident since for a given sampling effort (x-axis in Figure 4.18 and Figure 4.19) the species accumulation curve for '1 point per image' lies above '2 points per image' and so on.

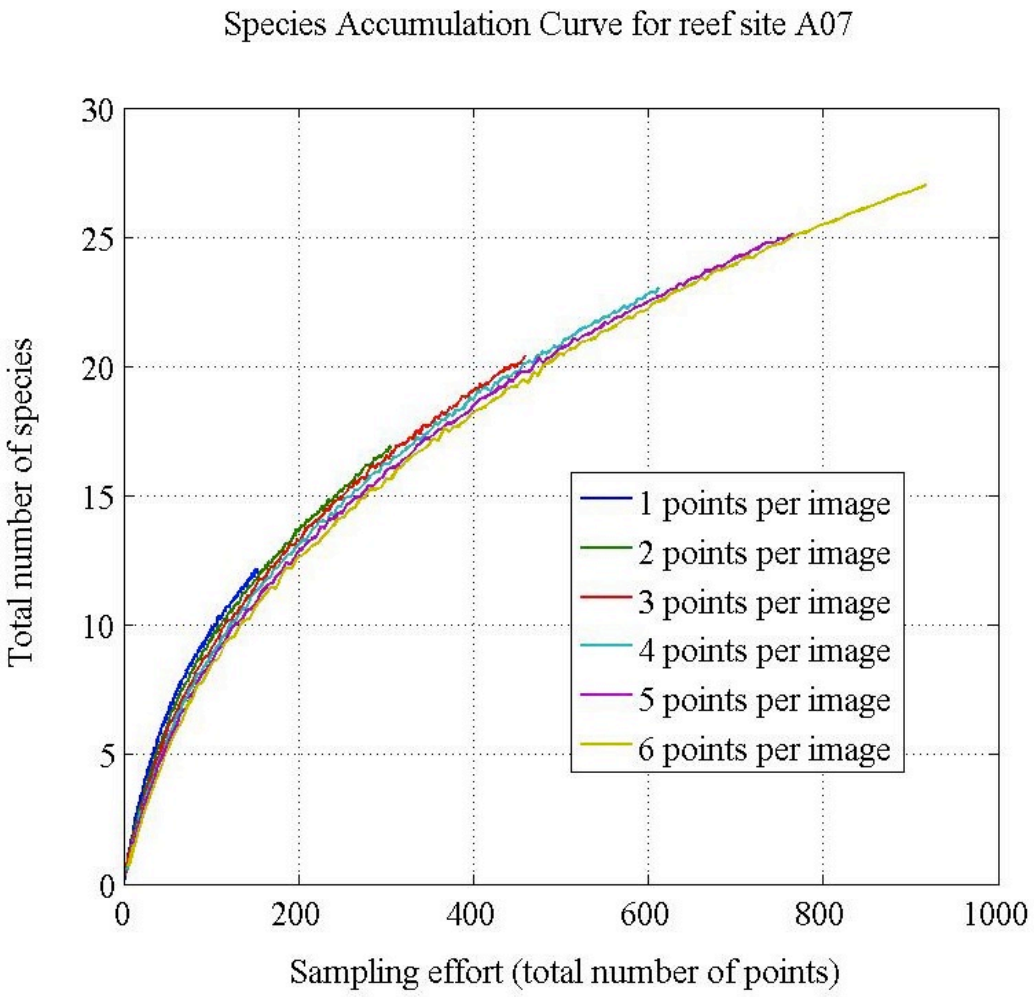


Figure 4.18 Species accumulation curves for reef site A7 for varying number of points (one to six) analysed per image. Images were selected randomly without replacement and points on each image were also selected randomly.

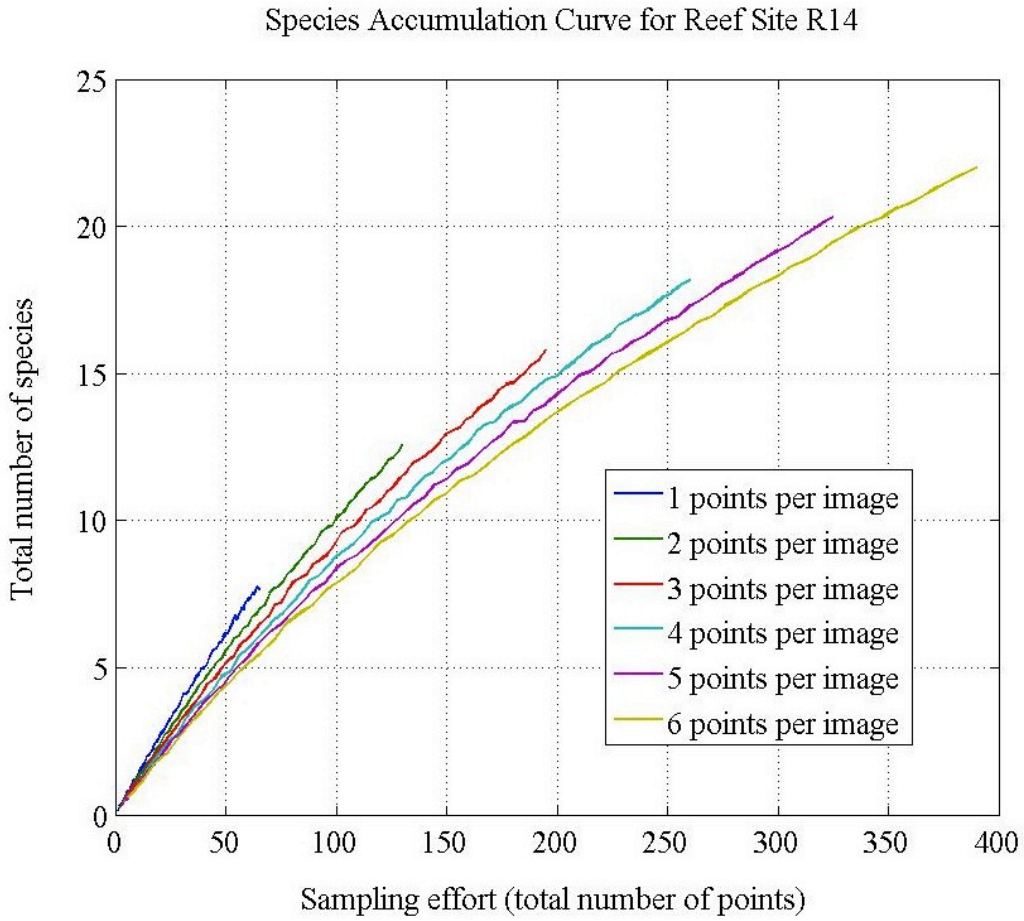


Figure 4.19 Species accumulation curves for reef site R14 for varying number of points (one to six) analysed per image. Images were selected randomly without replacement and points on each image were also selected randomly.

Mapping the species per unit effort (total number of species recorded divided by the number of identification points selected per image) against the number of points sampled per image indicates how many additional coral species are identified with each increase in sampling effort. For both site A07 (Figure 4.20) and R14 (Figure 4.21) it is clear that as the sampling effort increases, the benefit derived in terms of identifying additional coral species is reduced. This is confirmed when looking at box plots of the average number of species identified for each sampling effort for site A07 (Figure 4.22) and R14 (Figure 4.23).

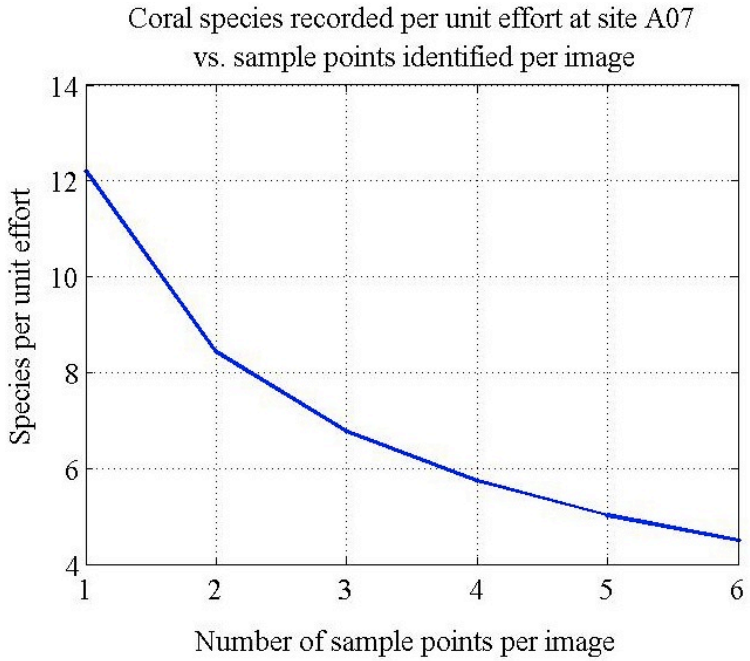


Figure 4.20 The number of coral species recorded per unit effort at sampling intensities ranging from one to six points per image at reef site A7. All points that do not contain a coral species (i.e. rubble, algae) are excluded from the analysis.

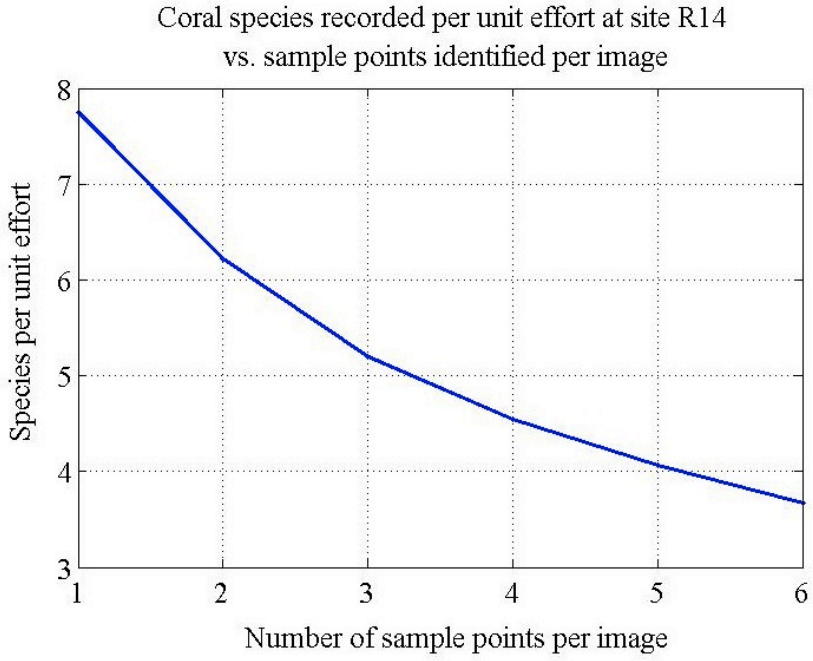


Figure 4.21 The number of coral species recorded per unit effort at sampling intensities ranging from one to six points per image at reef site R14. All points that do not contain a coral species (i.e. rubble, algae) are excluded from the analysis.

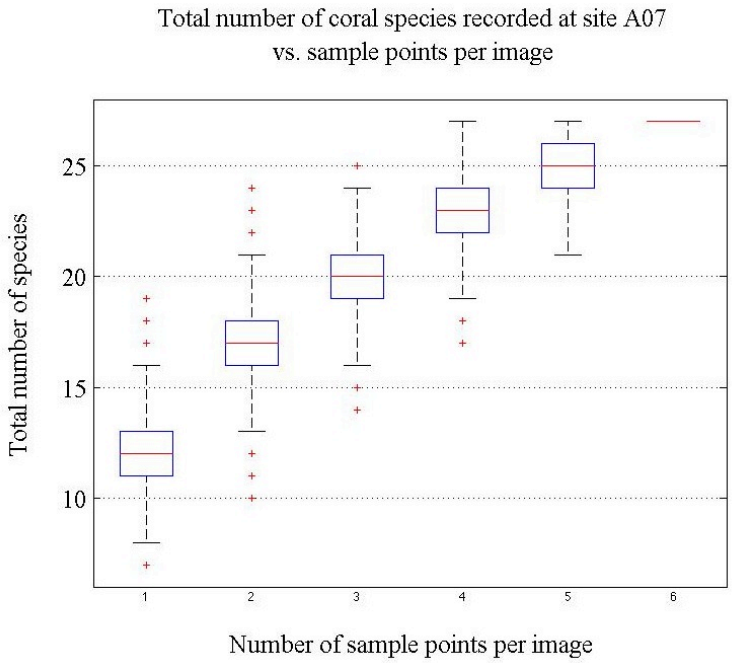


Figure 4.22 Box plot of the number of coral species recorded at reef site A7 for sampling efforts ranging from one point per image to six points per image.

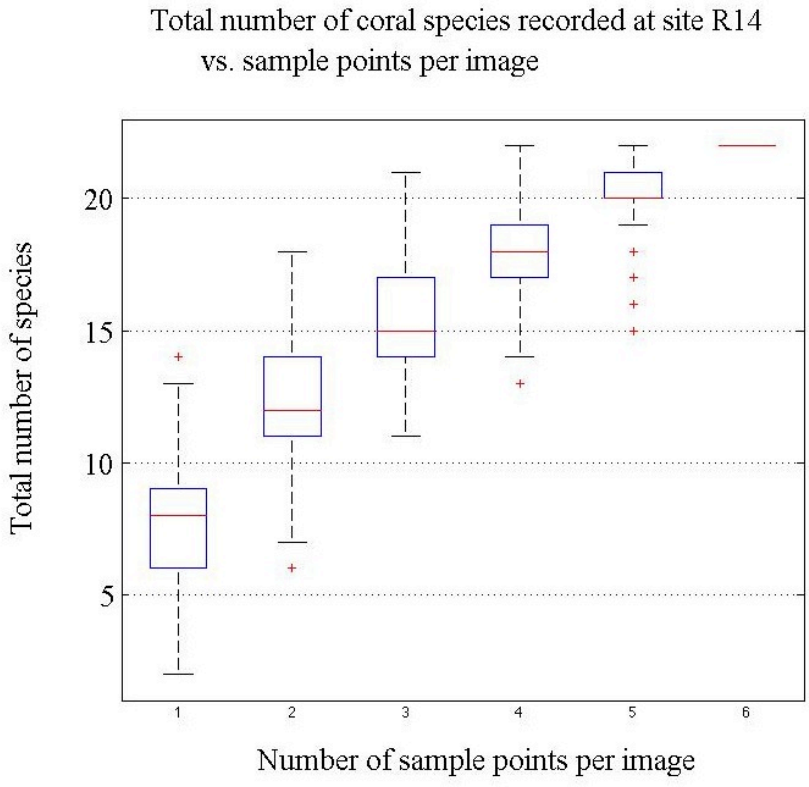


Figure 4.23 Box plot of the number of coral species recorded at reef site A7 for sampling efforts ranging from one point per image to six points per image.

4.6. Discussion

In this chapter the sampling objective, design, and field methodology including equipment, protocol, transect positioning, and depth zone selection was discussed. In addition the workflow used for processing photoquadrat images and linking them to GPS data was explained. The quantification of benthic composition using CPCe was demonstrated. Thereafter the database structure used for organizing all the collected data was presented. In addition the methodology used to replace species cluster level identifications with species level identifications was detailed.

In the second half of the chapter the issue of sampling effort as it relates to sampling area was discussed and the amount of data collected for each depth category was presented. The amount of data collected decreases with depth, as it is both expensive and occasionally dangerous to survey at depth. The ideal sampling effort per image was tested using a range of points per image and it was found that three points per image represented a good compromise between effort spent and data obtained.

5.
Emergent groups of *Scleractina* in Southwest Madagascar

5.1. Introduction

Groups of species with biological attributes that correlate with one another are referred to as emergent groups since they 'emerge' as clusters of species in trait space (Lavorel et al., 1997). Most often, clusters of species with similar sets of attributes have evolved to exploit a particular resource and can therefore be considered a guild. If the species comprising such a guild has similar influences on ecosystem processes it can be considered a functional group.

Testing for emergent groups is an important step to determining what trait-based methodologies are most useful for coral ecologists. For example, if clear emergent groups with no outliers for a given set of coral species exists, then very little additional information will be gained from surveys or analysis conducted on the species level. In other words, both surveys and analysis can be done at the emergent group level with confidence that inter-species trait variability is accounted for. If on the other hand all corals cannot be placed in emergent groups then one must (at the very least) survey the non-emergent group species as individual species.

Coral taxonomists have used clustering techniques on morphometric species-trait matrices to identify higher level taxa (i.e. Wallace, 1999), while others have done simple correlations between two (i.e. Porter, 1976) or three (i.e. Sebens, 1997) traits. However, I could find no study that explicitly tested for emergent coral groups using multiple non-morphometric traits.

Here the 231 species with biogeographic distributions in Southwest Madagascar are examined for emergent groups in terms of 26 *Scleractinan* traits (summarized in Table 5.1), comprising 136 attributes. This is done through translating the attributes into a binary matrix, calculating a weighted Gower dissimilarity coefficient and then using a range of clustering techniques to explore the membership and strength of emergent groups.

5.2. Methods

The traits identified for inclusion were determined through extensive examination of available taxonomic texts, published and grey literature (Chapter Two). Where traits were data poor in Southwest Madagascar they were not used. Traits not included were: larval size (seven percent data availability), planulae motility (six percent data availability) and egg size (three percent data availability). Also, data regarding colony polyp integration and aggressive hierarchies proved too sparse and/or vague for inclusion.

Table 5.1 to Table 5.3 list the 26 traits used in this study, their corresponding attributes, attribute weights, number of attributes per trait, attribute type, attribute symmetry, and the percentage of species in Southwest Madagascar for which data was available. Trait attributes are also identified as being either mutually exclusive (i.e. one trait can only have one attribute) or non-exclusive (i.e. one trait can have many attributes). The complete species-trait matrix with cited data sources for species in Southwest Madagascar is available in electronic form in Digital Supplement 1.1.3.

Table 5.1 Morphology traits, their attributes and attribute features.

		Trait	Attributes	Mutually exclusive attribute w/i trait	No. of attributes per trait	Attribute weight	Attribute type	Attribute asymmetry	% available for 231 species
Morphology	Colony level	Colony formation	colonial	Yes	1	1	binary	No	100
		Colony morphology	encrusting, submassive, massive, laminar (horizontal), laminar (vertical), foliose, freeliving,columnar or blades, tables,, corymbose, digitate, bushes, staghorn, bottlebrush, bushy coralliths, submassive coraliths	No	16	0.06	binary	Yes	100
		Maximum suface index	2.47, 3.2, 3.4, 5.9, 6.16, 6.43	Yes	6	0.167	binary	Yes	100
		Minimum surface index	2.47, 3.2, 3.4, 5.9, 6.16, 6.43	Yes	6	0.167	binary	Yes	100
		Morphological plasticity	Very high (SI range 3.03-3.96), High (SI range 2.5-2.96), Medium (SI range 0.2-0.53), low (SI range 0)	Yes	4	0.25	binary	Yes	100
		Attachment to reef	obligate freeliving, obligate attached, facultative freeliving	Yes	3	0.33	binary	Yes	100
		Colony growth strategy	determinate, indeterminate, semi-determinate	Yes	3	0.33	binary	Yes	100
		Maximum colony size	< 0.1 m, 0.1-0.3 m, 0.3-0.5 m, 0.5-1 m, 1-2 m, 2-3 m, 3-5 m, extensive stands	No	8	0.13	binary	Yes	100
	Corallite level	Corallite form	plocoid, sub plocoid, ceroid, scattered, phaceloid, flabellomeandroid, submeandroid, meandroid, hydnophorid, thamnasteroid, pachyseris type, freeliving monostomatous with axial furrow, freeliving polystomatous with axial furrow	No	13	0.08	binary	Yes	100
		Corallite spacing	crowded, fairly crowded, indistinct, well spaced, widely spaced	No	5	0.20	binary	Yes	100
		Corallite or valley width	< 1 mm, 1-5 mm, 5-15 mm, > 15 mm	No	4	0.25	binary	Yes	100
	Soft tissue level	Tentacle length	< 10 mm, 10-20 mm, > 20 mm	No	3	0.33	binary	Yes	100
		Polyp dimorphism	axial corallite, central corallite	Yes	2	0.50	binary	Yes	100
		Polyp colour	uniform-dull, center bright, wall bright, uniform bright	No	4	0.25	binary	Yes	100

Table 5.2 Behavioural traits, their attributes and attribute features.

		Trait	Attributes	Mutually exclusive attribute w/i trait	No. of attributes per trait	Attribute weight	Attribute type	Attribute asymmetry	% available for 231 species
Behaviour	Feeding related	Diel tissue expansion pattern	mantles extended by day, tentacle extended by day, vesicles extended by day, no expansion by day	No	4	0.25	binary	Yes	100
		Daytime tissue projection	< 1 mm, 1-5 mm, 5-20 mm, > 20 mm	No	4	0.25	binary	Yes	100
	Sediment shedding	Active sediment shedding ability group	1A, 1B, 1C, 2, 3, 4, 5, 6	Yes	7	0.14	binary	Yes	13

Table 5.3 Physiological traits, their attributes and attribute features.

		Trait	Attributes	Mutually exclusive attribute w/i trait	No. of attributes per trait	Attribute weight	Attribute type	Attribute asymmetry	% available for 231 species
Physiological	Sexual reproduction	Sexuality	hermaphroditic, gonochoric, mixed breeding	Yes	3	0.33	binary	Yes	69
		Larval development	brooder, spawner	No	2	0.50	binary	No	68
		Spawning behaviour	slow gamete extrusion, vigorous gamete ejection, passive gamete release	No	3	0.33	binary	Yes	28
	Asexual reproduction	Asexual reproductive mode	fragmentation, anthocaulus budding, asexual brooder, polyp balls, polyp bailout	No	5	0.20	binary	Yes	100
		Intra-colony budding pattern	extratentacular, intratentacular, incomplete intratentacular, hydnophorid, thamnasteroid	No	5	0.20	binary	Yes	100
	Environmental sensitivity	Symbiont clade association	A, B, C, D	No	4	0.25	binary	No	60
		Hardiness	med-high susceptibility to bleaching, med-high susceptibility to disease, med-high susceptibility to predation, med-high resistance to bleaching, med-high resistance to disease, recovers quickly from bleaching or disease	No	6	0.17	binary	No	94
	Larval biology	Larval symbiont association	larval symbionts present	Yes	1	1.00	binary	No	54
		Egg colour	apricot, aqua, blue, brown, cream, green, grey, grey-brown, lavender, orange, pink, purple, red, tan, white, yellow	No	16	0.06	binary	Yes	26

All trait attributes were recoded as binary variables. Binary trait attributes proved useful for translating vague statements in taxonomic text such as "colony often over two metres" to binary variables such as 'two to three metre colony diameter' = 1. Also, using binary attributes aided in coding data from the electronic taxonomic key Coral ID (Veron and Stafford-Smith, 2002) where continuous traits such as corallite width are available as ranges (i.e. one to five mm). One caveat when coding continuous traits as categorical by using size range bins is that species with a widely variable attribute (eg. calice width) may appear to have lower trait plasticity than a species with less variability for the same trait.

For example, corallite width is a continuous trait measurement (mm) that was listed as categorical by Veron (i.e. less than 1 mm, 1 - 5 mm, 5 - 15 mm, greater than 15 mm) and was kept in this format for simplicity. Under this category scheme a species with a valley width ranging from 1.1 to 4.9 mm would have only one attribute while a species with a valley width of 4.9 to 5.1 mm would have two attributes. Therefore multiple trait attributes do not directly reflect trait plasticity for the four traits that were continuous but coded as binary trait attributes: maximum colony size, corallite size, tentacle length, and daytime tissue projection.

Each trait attribute had two possible outcomes: 1 (attribute present in species) and 0 (attribute not present in species). A binary variable was considered symmetric when there was no preference for which outcome should be coded as 0 or 1, in other words, both 0 and 1 'mean' something. When using symmetrical binary variables in calculations of similarity coefficients both 1-1 and 0-0 matches imply similarity.

Five traits had symmetrical trait attributes: colonality, larval development, symbiont clade association, larval symbiont association, and hardiness. A brief explanation of why these five traits were considered symmetric follows.

'Colonality' is symmetrical since the absence of this trait implies that the coral is solitary, which is ecologically meaningful. 'Larval development' has two attributes 'brooder' and 'spawner' which are non-exclusive (that is, some corals can both brood and spawn). Therefore, if brooder = 0 a species must be a spawner and vice versa, thus, 0 has meaning. Likewise, if brooder = 1 a species can brood and possibly

also spawn and vice versa, thus, 1 has meaning. 'Symbiont clade association' has four non-exclusive trait attributes (i.e. corals can theoretically associate with any combination of clade A, B, C, and D). Both the ability and inability to associate with each clade (A-D) strongly influences the ability of a coral species to inhabit particular environmental niches and thus both 1 and 0 have ecological meaning. 'Hardiness' has six non-exclusive attributes based on observations of the susceptibility, resistance and recovery ability of corals from bleaching, disease, and predation (Carpenter et al., 2008). If 'medium to high susceptibility to bleaching' = 0 it indicates that the coral has low susceptibility to bleaching. 'Larval symbiont association' has only one attribute 'larval symbiont present' whose presence or absence (1 or 0) both has implications for larval metabolic competency and therefore dispersal distance.

The attributes of the remaining 21 traits are asymmetric. When using asymmetrical binary variables in calculations of similarity coefficients a 1-1 match implies similarity while 0-0 does not. For example, for the trait 'corallite form' and the attribute 'thamnasteroid corallite form' species with thamnasteroid corallite form are considered similar but species without thamnasteroid corallite form are not considered similar.

While the coding of most traits was straight-forward (i.e. attachment to reef, 1 = yes, 0 = no) and are detailed sufficiently in Chapter Two, the coding of several traits requires further explanation, which is done in the following section.

5.2.1. Comments on trait coding to 1-0 matrix

Surface index, while a continuous trait, has to date only been calculated for six major colony morphologies (Holmes, 2008). Therefore, the 16 colony morphology attributes were translated into Holmes' six SI values (summarized in Table 5.4). This allowed the minimum, maximum and morphological plasticity (SI range) of surface indices for each coral species to be recorded. While admittedly crude, this use of SI scores allows quantification of the simplest growth form (minimum SI), most complex growth form (maximum SI) and growth form plasticity (SI range).

Table 5.4 Conversion table for translating colony growth morphologies into surface index (SI) scores (Holmes, 2008).

Holmes Growth morphology	**SI**	**Morphologies in this study**
Massive	3.2	massive, submassive coralliths
Sub-massive	5.9	encrusting, submassive, laminar (horizontal), freeliving,
Foliose	3.04	laminar (vertical), foliose, columnar
Open branching	6.16	corymbose, digitate, staghorm
Complex branching	6.43	bushes, bottlebrush, bushy coralliths
Tabular	2.47	tables

Colony growth strategy had three mutually exclusive attributes: indeterminate, semi-determinant, and determinate. Attribute assignment for *Acropora* was done using the taxonomic revision of *Acropora* by Wallace (1999). Wallace lists *A. florida, A. latistella, A. loripes, A. monticulosa, A, polystoma, A. valida, A. vermiculata* as having both determinant and indeterminate growth but did not explain further what she meant by this dual classification. Using additional taxonomic texts (Veron and Wallace, 1984) and images these species were reclassified as follows: 1) indeterminate growth (*A. florida*) 2) semi-determinate growth (*A. latistella, A. monticulosa, A. polystoma, A. valida, A vermiculata*), and 3) determinate growth (*A. loripes*).

Maximum colony size was coded from taxonomic texts, which sometimes used phrases such as 'rarely over one metre across' and 'often over 0.5 m.' To accommodate such phrasing 8 discreet size classes were used (< 0.1 m, 0.1 - 0.3 m, 0.3 - 0.5 m, 0.5 - 1 m, 1 – 2 m, 2 - 3 m, 3 - 5 m, and extensive stands) and the size class immediately greater than the statement was selected (i.e. 'often over 0.5 m' was coded as '0.5 - 1 m' = 1). Maximum colony size is not a mutually exclusive trait since species with semi-determinate growth have both a maximum diameter size for subunits (i.e. plates) and also form 'extensive stands'. All colonies recorded as having indeterminate growth strategies were also listed as forming extensive stands.

In regards to maximum colony size a number of diversions from taxonomic text listings were taken. In Madagascar the following species were not observed to exceed 0.3 metres in diameter and always formed small distinct bushes: *Pocillopora*

damicornis, Pocillopora eydouxi, Pocillopora indiania, Pocillopora verrucosa, Seriatopora hystrix, Stylophora pistilata, Stylophora subseriata, Stylophora wellsi and were all coded as having a maximum colony size of '0.1 - 0.3 m' = 1. These eight species are listed by Veron (2000) as having the following maximum colony sizes: "able to form extensive stands" (*S. hystrix*), "colonies are compact clumps reaching several metres across" (*P. damicornis*), "often over one metre across" (*P. eydouxi* and *P. indiania*), "seldom more than 0.5 m across" (*P. verrucosa)*. Characteristic growth sizes were not listed for *S. pistillata, S. subseriata,* and *S. wellsi.*

Polyp dimorphism was treated as a trait with three exclusive asymmetrical attributes: 'axial corallite present', 'central corallite present', 'neither axial nor central corallite present'. Veron (2002) lists 19 of the 64 *Acropora* species present as having both an 'axial corallite present' and having 'neither axial nor central corallite present'. This dual classification is presumably because while all *Acropora* species have axial corallites, sometimes these are difficult to distinguish (as in plates such a *A. lamarcki* and heavily fused branches such as *A. irregularis*). The 19 *Acorpora* species with dual classifications are treated here as having 'axial corallites present' and therefore all *Acropora* species, and only *Acropora* species, have this trait attribute.

In total 11 species from three families (*Pectiniidae, Fungiidae,* and *Agaricidae*) were listed as having a 'central corallite present' and 'neither axial nor central corallite present' (Veron and Stafford-Smith, 2002) likely reflecting the fact that these coral species sometimes exhibit a central corallite and sometimes do not. Here these 11 species were treated as having a central corallite.

Larval development mode has two non-exclusive symmetrical binary attributes: spawning and brooding. The attributes are non-exclusive because four of the species present in the region both spawn and brood: *Goniastrea aspera* (Sakai, 1997), *Pocillopora damicornis* (Glynn et al., 1991, Tanner, 1996), *Leptastrea purpurea* (Hayashibara et al., 1993, Peter Schupp personal communication to Baird et al., 2009) and *Fungia fungites* which is a gonochoric brooder in Okinawa (Loya et al., 2009) and a spawner on the GBR (Willis et al., 1985).

Diel tissue expansion had four non-exclusive, asymmetrical binary attributes indicating if: mantles, tentacles, vesicles or no tissue is extended by day. Data was available for all species and was taken from Veron (2002) who listed some species as having both 'no tissue extended by day' and 'mantel, tentacles, or vesicles expanded by day'. This was interpreted as flexibility in whether or not a species expands tissues during the day. For example, species with 'tentacles expanded by day' = 1 and 'no expansion by day' = 0 were assumed to *always* have their tentacles expanded (i.e. *Polyphyllia talpina*) while species with 'tentacles expanded by day' = 1 and 'no expansion by day' = 1 were assumed to *sometimes* have their tentacles expanded by day.

5.2.2. Selection of distance measure

While a plethora of distance measurements are available in ecology (Bray-Curtis, Jaccard, etc.), only two have been recommended for the measurement of interspecific dissimilarity based on trait values: Euclidean distance (i.e. Petchey and Gaston, 2002) and Gower distance (i.e. Podani and Schmera, 2006). Of these two only Gower distance (Gower, 1971, Podani, 1999, Villéger et al., 2008) allows for binary asymmetric data, missing trait data, and weighting of traits. For these reasons the Gower similarity was chosen as a distance measurement for this study.

The Gower similarity was calculated using the *gowdis* function of the FD package in the R-platform (Laliberté and Legendre, 2010) as follows:

$$G_{jk} = \frac{\Sigma_{i=1}^{n} w_{ijk} s_{ijk}}{\Sigma_{i=1}^{n} w_{ijk}}$$

were w_{ijk} is the weight of the trait attribute i for the j-k species pair, and s_{ijk} is the partial similarity of trait attribute i for the j-k species pair. For symmetric binary variables w_{ijk} and $s_{ijk} = 0$ if species j and k cannot be compared because trait attribute data is unavailable for either or both species, and $s_{ijk} = 1$ if $x_{ij} = x_{ik} = 1$ or if $x_{ij} = x_{ik} = 0$. For asymmetric binary variables calculations are made the same as above except that $w_{ijk} = 0$ if $x_{ij} = x_{ik} = 0$.

5.2.3. Selection of weighting scheme

Deciding if and how to weight the traits when calculating similarity coefficients has proved a controversial problem for taxonomists (Gower, 1971) and for those calculating trait diversity metrics. As pointed out by Somerfield et al. (2008), in their presentation a novel trait-based index which they illustrated using North Sea fish, the number of categories used to code a continuous variable (i.e. tentacle length) results in an implicit weighting for that trait in the next step of the analysis. Their approach was to equally weight all trait-attributes (i.e. equal weighting is placed at the W1 level in Table 5.5) and to limit the categories used to code continuous variables to four. However, whilst they rationalized that traits should not be weighted, as one often does not know before-hand which traits might be important, they admit their approach implicitly weights traits by the number of attributes used to code them thereby inflating the importance of traits with many attributes.

Laliberte and Legendre (2010) suggested that in order to avoid overweighting traits with many attributes, each trait should be weighted equally and each attribute weighted by the original weight of the trait divided by the number of binary variables required to recode it (i.e. equal weighting is placed at the W2 level in Table 5.5).

It is also possible to position the equal weighting even further up the 'trait-tree' by placing equal weight on trait categories (i.e. equal weighting is placed at the W3 level in Table 5.5) or on major trait categories (i.e. equal weighting is placed at the W4 level in Table 5.5).

Table 5.5 The four levels at which equal weighting was tested: W1) Attribute level, W2) Trait level, W3) Trait category level, W4) Major trait category level. For brevity the attributes are not listed here but counted. Attributes for each trait is listed in Table 5.1 to Table 5.3.

Major trait categories (W4)	**Morphology**													**Physiological**										**Behaviour**		
Trait categories (W3)	**Colony level**								**Corallite level**			**Soft tissue level**			**Sexual reprod.**			**Asexual reprod.**		**Env. sensitivity**		**Larval biology**		**Feeding**		**Sediment shedding**
Traits (W2)	Colonality	Colony morphology	Minimum surface index	Maximum surface index	Morphological plasticity	Reef attachment	Colony growth strategy	Maximum colony size	Corallite form	Corallite spacing	Corallite size	Tentacle length	Polyp dimorphism	Polyp colour	Sexuality	Larval development	Spawning behaviour	Asexual reproductive mode	Intra-colony budding pattern	Symbiont clade association	Hardiness	Larval resilience	Egg colour	Diel tissue expansion pattern	Daytime tissue projection	Active sediment shedding group
No. Attributes (W1)	**1**	**16**	**6**	**6**	**4**	**3**	**3**	**8**	**11**	**5**	**4**	**3**	**2**	**4**	**3**	**2**	**3**	**5**	**5**	**4**	**6**	**1**	**16**	**4**	**4**	**7**

To examine how equal weighting at different levels of the 'trait-tree' (Table 5.5) influence clustering of species into emergent groups, the four different weighting schemes W1 - W4 were applied. The resulting Gower dissimilarity matrices were coloured by value intensity and reordered using the unweighted pair-group method using arithmetric averages clustering method (hereafter UPGMA), which was found to be the most appropriate clustering method for the dataset (described later). The resulting 'ordered heatmaps' for weighting scheme W1 - W4 are shown in Figure 5.1.

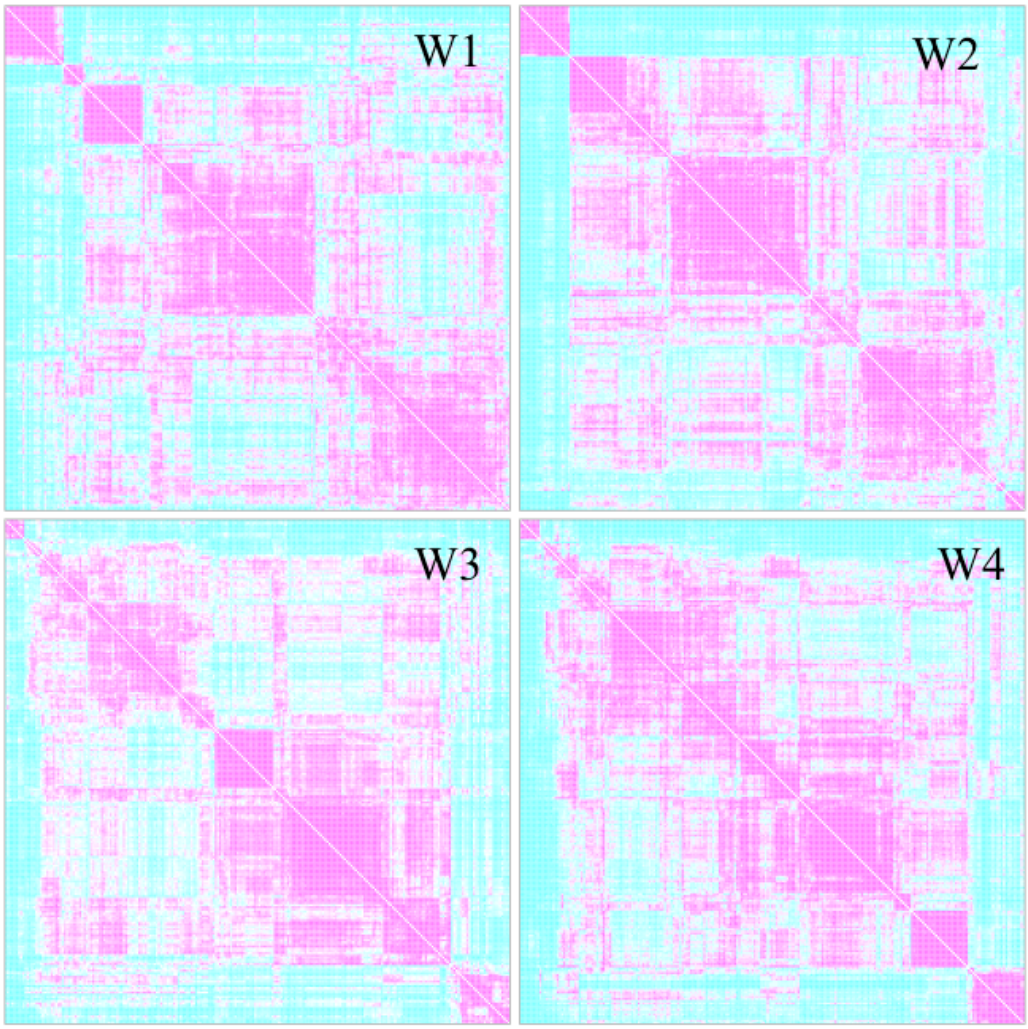


Figure 5.1 Heat maps of the Gower dissimilarity matrices for the 231 species present in this study with the different weighting schemes W1 - W4 indicated. Magenta indicates trait dissimilarities between species close to zero (maximum similarity) while cyan indicates trait dissimilarities between species close to one (minimum similarity). Species are ordered by dendrogram position resulting from UPGMA clustering. Note that as weighting is moved up the 'trait tree' (i.e from W1 to W4) more groups become apparent along the diagonal.

It is clear from the ordered dissimilarity matrices (Figure 5.1) that as the weighting moves 'up the trait organization tree' (i.e. from W1 to W4) more and tighter groupings appear. This is because if weighting is applied further down the trait tree (i.e. W1 and W2) more emphasis is placed on rare trait attributes (for example *Diploastrea heliopora*'s 'mixed breeding system' attribute for the trait 'sexuality') and thus the heat map becomes more diffuse.

The rarity of the 136 trait attributes is summarized in Appendix Six. Interestingly, the most rare trait attributes are not found in most rare species. For example, the attribute asexual brooder occurs only in one species, *Pocillopora damicornis*, yet this species was very abundant especially on shallow spur and groove systems in Southwest Madagascar. Likewise the expansion of vesicles during the day is very rare and only occurs in *Physogyra lichtensteini* and *Plerogyra sinuosa*, yet these corals can be very abundant particularly in sediment rich environments.

In searching for emergent groups one must decide at which level (W1 - W4) it is most appropriate to weight species traits. The W4 weighting scheme seemed to force species into clusters too harshly while the W1 weighting scheme resulted in clustering of only the most self-similar genera (*Cycloseris/Fungia*, *Montipora, Goniopora/Alvepora*). The W2 and W3 weighting schemes were good intermediates between these extremes and were therefore both used in the subsequent analyses.

5.2.4. Selection of clustering method

There is lack of agreement over which clustering method best represents the distribution of species in trait space (Podani and Schmera, 2006). Mouchet et al. (2008) showed that due to the complexity of interactions between correlations of traits, distance measures and clustering methods no combination of clustering method and distance measure consistently outperforms another. They suggested therefore that for each unique dataset all possible combinations of distance measurements and clustering methods should be tested to determine which method is most suitable. Therefore seven common clustering models were tested: 1) single linkage agglomerative clustering 2) complete linkage agglomerative clustering 3)

unweighted pair-group method using arithmetic average -UPGMA 4) unweighted pair-group method using centroids –UPGMC 5) weighted pair-group method using arithmetic averages –WPGMA 6) weighted pair-group method using centroids – WPGMC and 7) Ward's minimum variance clustering.

5.2.4.1. Cophenetic Correlations

In order to determine which clustering model best represented the original Gower dissimilarity matrix the cophenetic correlations were calculated between the original Gower dissimilarity matrix and the seven clustering models. The cophenetic correlation (also referred to as the cophenetic correlation coefficient) is a useful measure of how closely a dendrogram preserves the pairwise distances calculated between the original objects (in this case species).

The cophenetic correlation is the Pearson's *r* correlation between the original dissimilarity matrix and the cophenetic matrix. A cophenetic matrix is a matrix of the cophenetic distances between all species. The cophenetic distance is determined by starting at one species and then 'climbing up the tree' to the first node that leads down to the second species. The position of that node along the distance scale is the cophenetic distance between the two species.

The cophenetic correlations were calculated between the seven clustering models and the original Gower dissimilarity matrix (which summarises the Gower dissimilarities between species in terms of their associated traits). The cophenetic correlations of the seven clustering methods were tested for both the W2 and W3 weighting schemes and the resulting 14 plots are available in Appendix 7.1 and 7.2. It was found that for both weighting schemes, the UPGMA clustering model had the highest cophenetic correlation (W2 = 0.845 and W3 = 0.8; Figure 5.2).

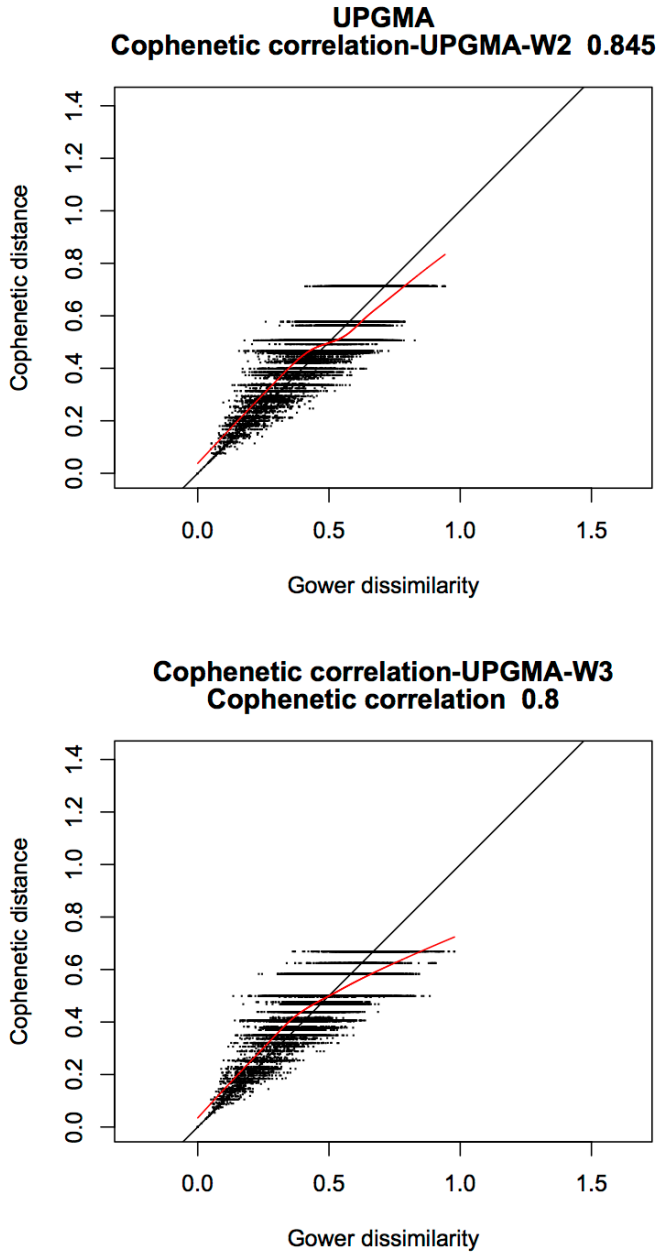


Figure 5.2 Cophenetic correlations for UPGMA clustering using W2 and W3 weighting schemes. The cophenetic distance matrix tests how well clustering methods represent the original Gower distance matrix. A LOWESS smoother shows the trend in each plot. A higher correlation value indicates that the clustering model is better at representing the original distance matrix. This type of correlation cannot be tested for significance and is simply a tool for selecting the most appropriate clustering method.

5.2.5. Identifying interpretable clusters

Potential emergent species clusters were extracted from the dendrogram. This required that a decision be made regarding the height at which the dendrogram should be cut. In other words, the height at which groups within the dendrogram are 'true' groups. In order to help determine a suitable cutting height, fusion levels were plotted for the UPGMA clustering method for both the W2 and W3 Gower dissimilarity matrices (Figure 5.3). The fusion level is simply the height at which a fusion between two branches occurs in the dendrogram.

It is clear that for both the W2 and W3 weighting scheme, increased clustering occurred between around five and 35 groups. This was also the case for the fusion plots of the other six clustering methods tested for both weights (available in Appendix 7.3 and 7.4). Therefore this break in the curve was examined in more detail (Figure 5.4). For both weighting schemes there appeared to be a break in the curve around five to six groups and again around 15.

In order to further facilitate the decision of dendrogram cutting position contingency tables were used to compare all 42 combinations of the seven clustering methods and two weighting schemes. If two clustering methods produced the same groups at a given cutting level only one non-zero value would be present for each row. Since the fusion tables tended to increase sharply between five and 35 clusters, contingency tables were examined for this range of cutting levels. No two clustering methods resulted in identical groups at any cutting level although many resulted in nearly identical groupings at group sizes of six and 15.

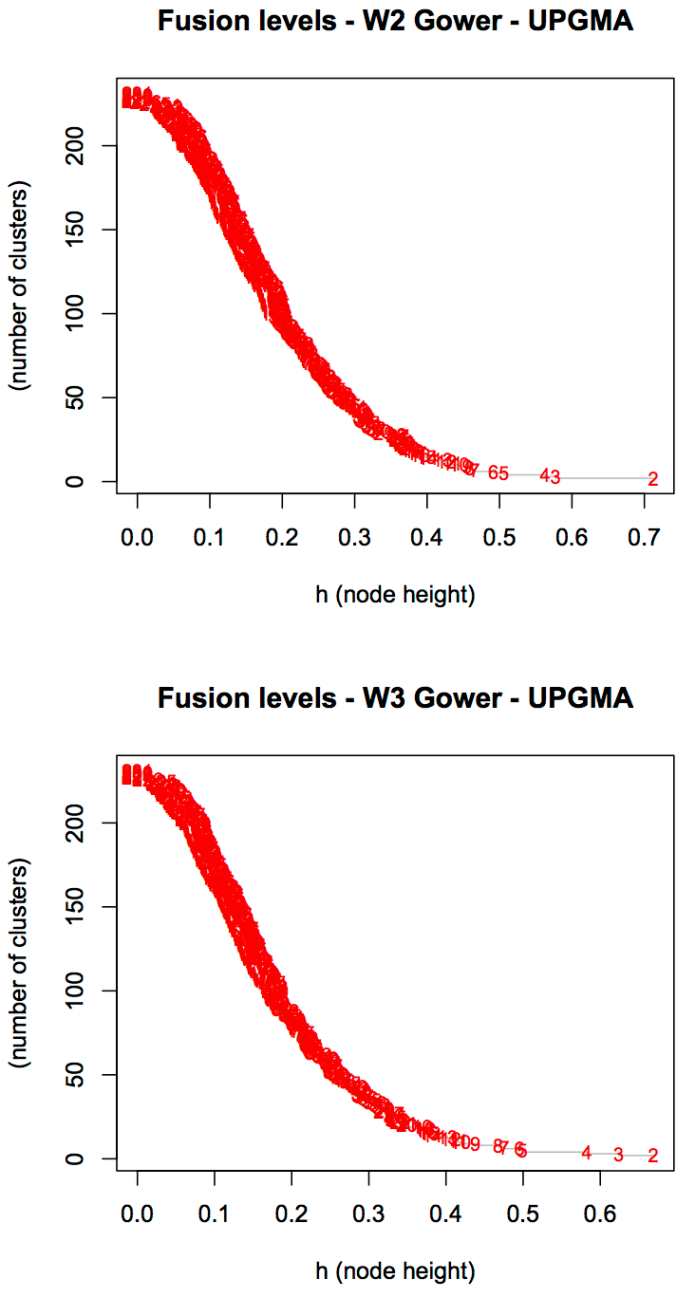
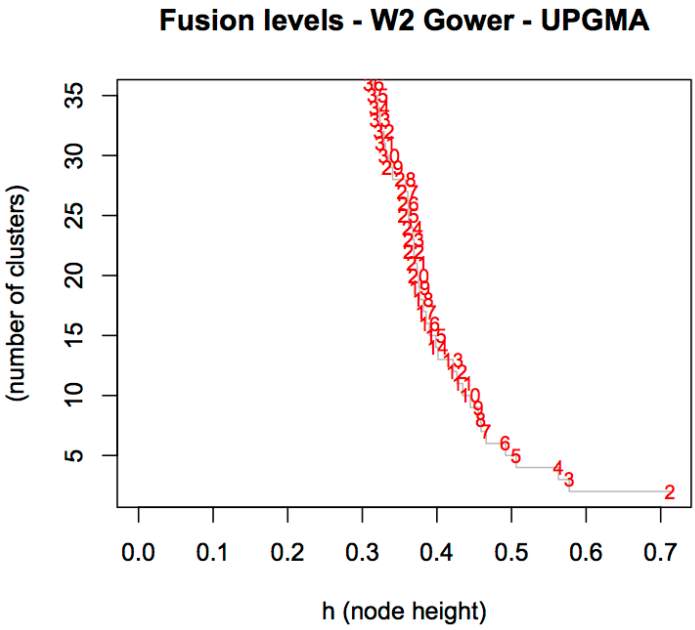


Figure 5.3 Plots of the levels of dissimilarity (node height) at which groups are fused. Fusion levels for UPGMA clustering models on both the W2 and W3 weighted Gower dissimilarity matrix are shown. All possible numbers of clusters (i.e. all fusion in the dendrogram) are shown.



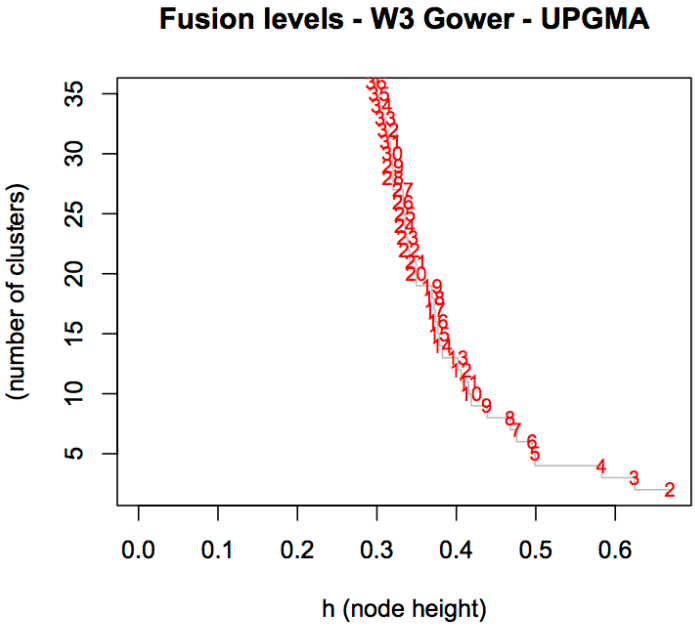


Figure 5.4 Plots of the levels of dissimilarity (node height) at which groups are fused. Fusion levels for UPGMA clustering models on both the W2 and W3 weighted Gower dissimilarity matrix are shown. A maximum of 35 clusters (i.e. the top the dendrogram) is shown.

To determine the degree of coherence between species in a group, at different dendrogram cutting levels, silhouette widths are useful. For a given number of groups the average silhouette widths per group can be used as an indication of how strong the within-group links are as compared to the between-group links. Silhouette widths can range between -1 and 1, with negative values indicating that species are likely to have been placed in the wrong cluster. The largest average silhouette width indicates the number of groups at which within-group linkage is the strongest.

Silhouette widths were calculated for all the clustering methods and both weighting schemes and the resulting 14 plots are available in Appendix 7.5 and 7.6. For both weighting schemes, single, UPGMC, and WPGMC clustering methods produced negative silhouette widths for many cutting levels, confirming that these clustering methods are not appropriate for this dataset. Complete, UPGMA, WPGMA, and ward clustering produced groups with positive and large silhouette widths. This further confirmed that UPGMA was a good clustering method choice.

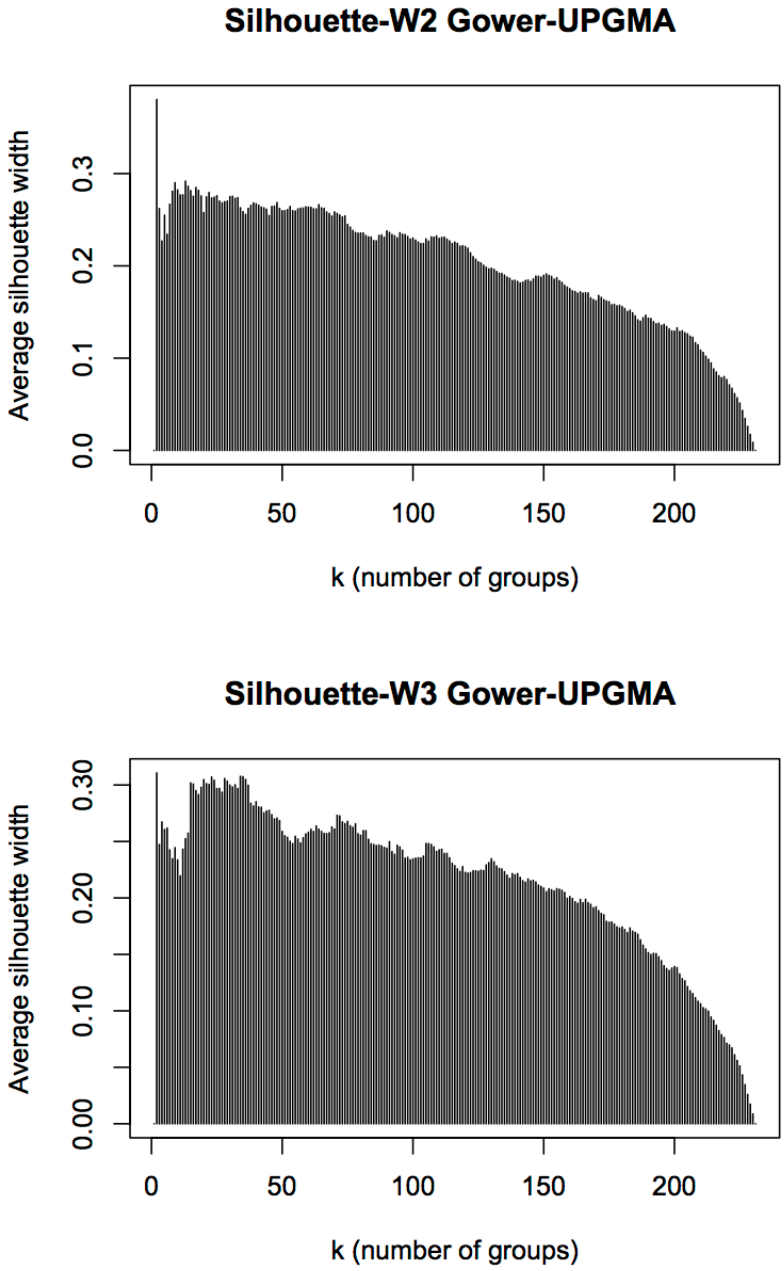


Figure 5.5 Average silhouette widths for groups at different cutting levels (k) along the dendrogram. The UPGMA clustering of species in terms of the W2 and W3 weighted Gower dissimilarity measures are shown. Greater widths show greater cluster coherence.

Since most clustering methods showed the strongest clusters when the cutting level was below 35 groups this section of the silhouette plot was examined more closely (Figure 5.6). A group size of 15 was selected since this cut-off produced the largest

silhouette width for UPGMA (Figure 5.6) with the exception of two, which would have resulted in ecologically unreasonable grouping. The UPGMA clustering method was chosen for subsequent analysis as it had the highest cophenetic correlation and consistently produced fairly well balanced and well-defined groups.

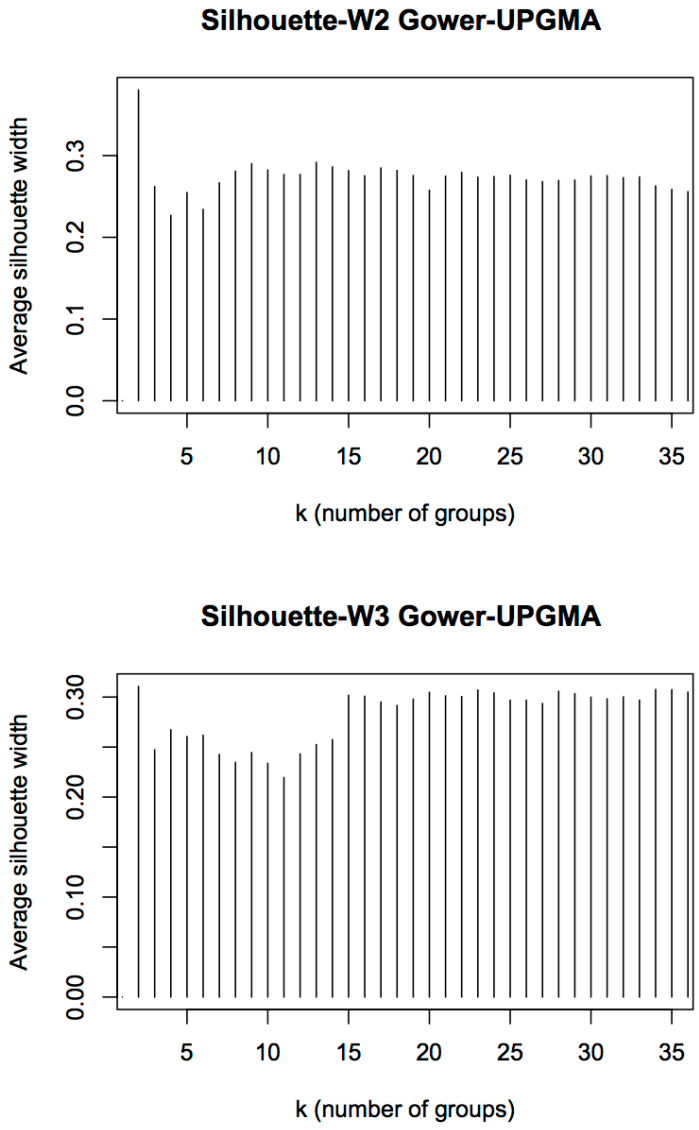


Figure 5.6 Average silhouette width Silhouette graphs for groups at different cutting levels (1 to 35) along the dendrogram. The UPGMA clustering using the W2 and W3 weighted Gower dissimilarity is shown. Greater widths show greater cluster coherence.

5.3. Results

A heat map of the W2 Gower dissimilarity matrix gives a representative initial overview of the trait similarities of the coral species in the region (Figure 5.7). Since species are listed in alphabetical order from top to bottom along the left-hand axis, and from left to right along the top axis, genus self-similarity in terms of traits is shown on the diagonal. It is clear that particular genera are highly self-similar while others are more diffuse. Genera with high levels of self-similarity include: *Acropora, Montipora, Cycloseris,* and *Fungia.* The heat map did not change greatly when the traits that had missing values were removed (eight of 26 traits) confirming that the Gower distance measurement can indeed handle missing data well. The alphabetic heat map of the W3 Gower dissimilarity matrix was very similar to the W2 Gower dissimilarity matrix and is therefore not shown.

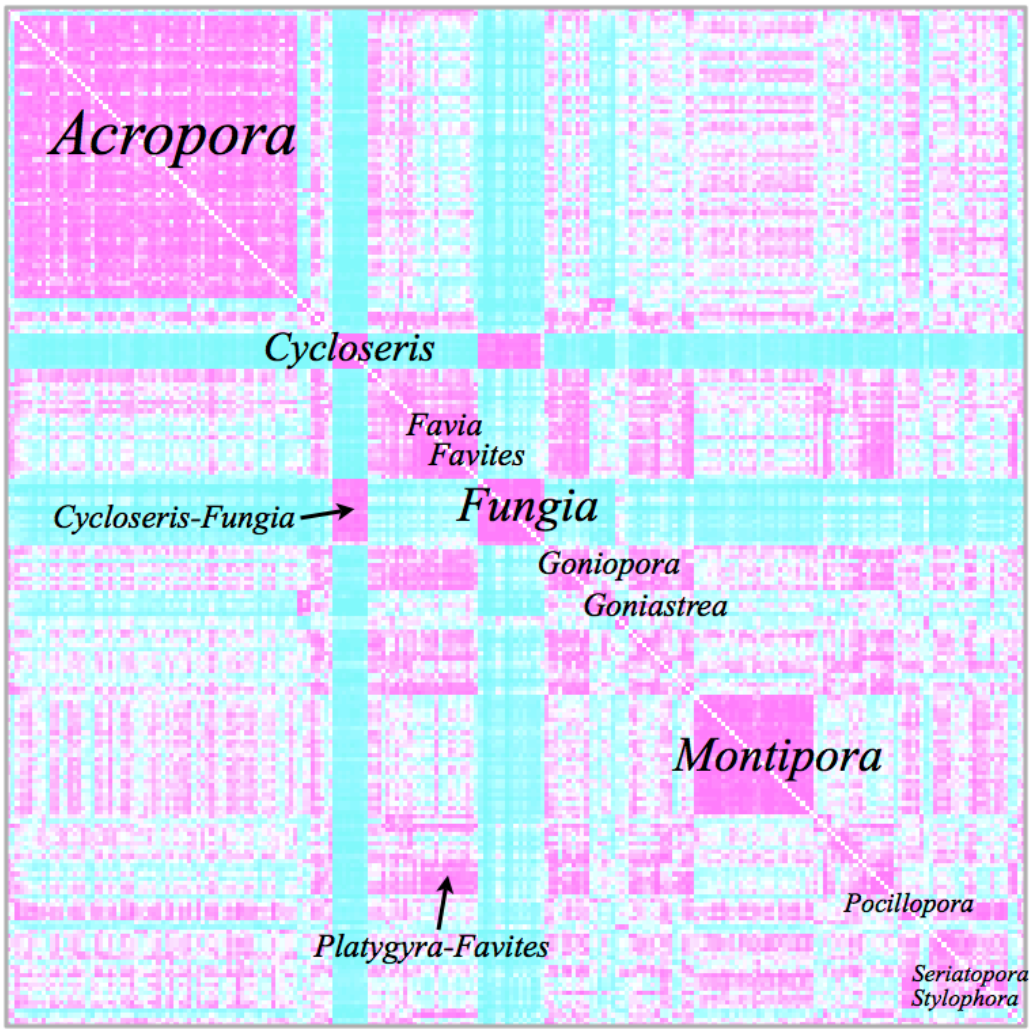


Figure 5.7 Heat map of W2 Gower dissimilarity for the 231 species present in Southwest Madagascar. Magenta indicates trait dissimilarities between species close to zero (maximum similarity) while cyan indicates trait dissimilarities between species close to one (minimum similarity).

5.3.1. Emergent groups-equally weighted traits (W2)

Potential emergent groups are visible as red hot spots on a heatmap of the Gower dissimilarity matrix reordered according to the dendrogram resulting from the UPGMA clustering method (Figure 5.8). The candidate emergent groups are outlined in black and labelled. A plot of silhouette width shows the coherence of the candidate emergent groups (Figure 5.9). The labels and numbers in these two figures are referenced in the description of emergent groups that follows.

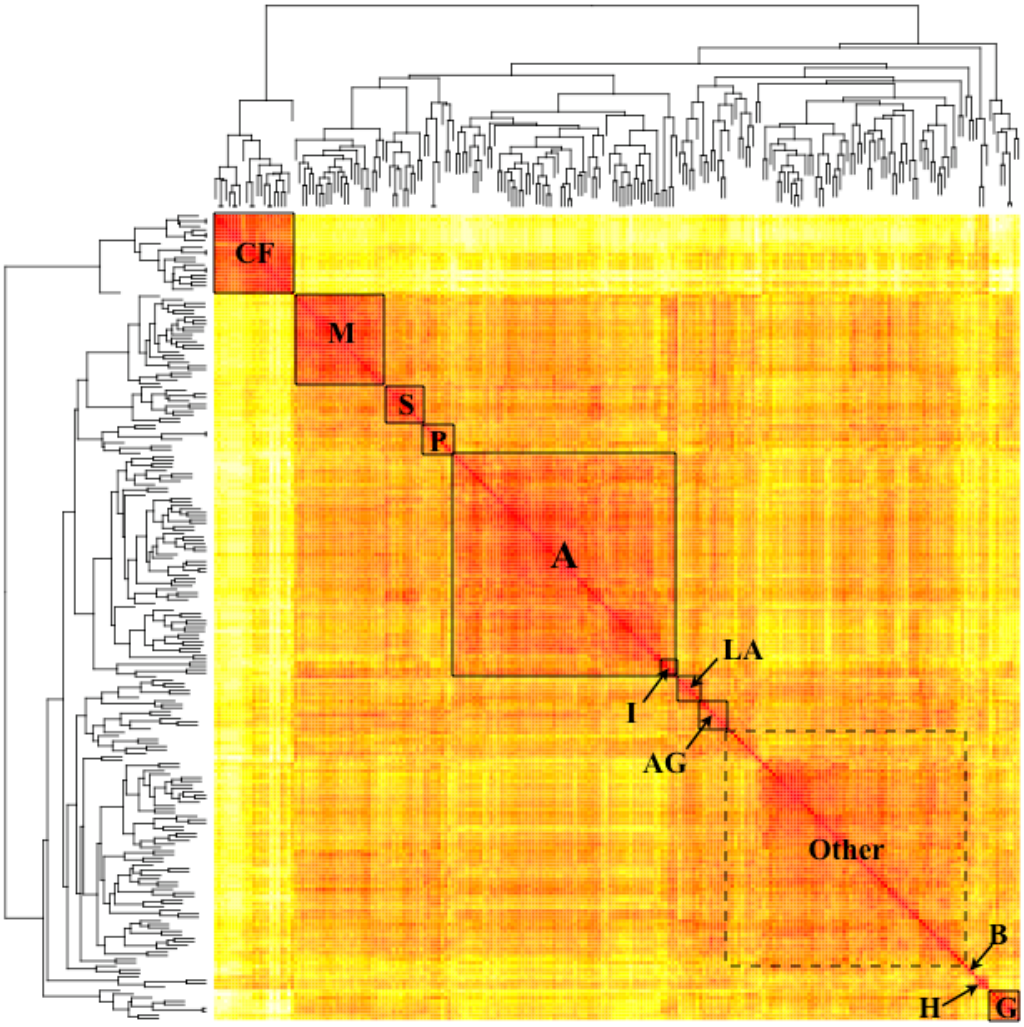


Figure 5.8 W2 weighted Gower dissimilarity matrix for the 231 species in Southwest Madagascar reordered by the dendrogram resulting from the UPGMA clustering. Red area areas indicate groups of species with high trait similarity. The labels refer to the emergent groups described in-text.

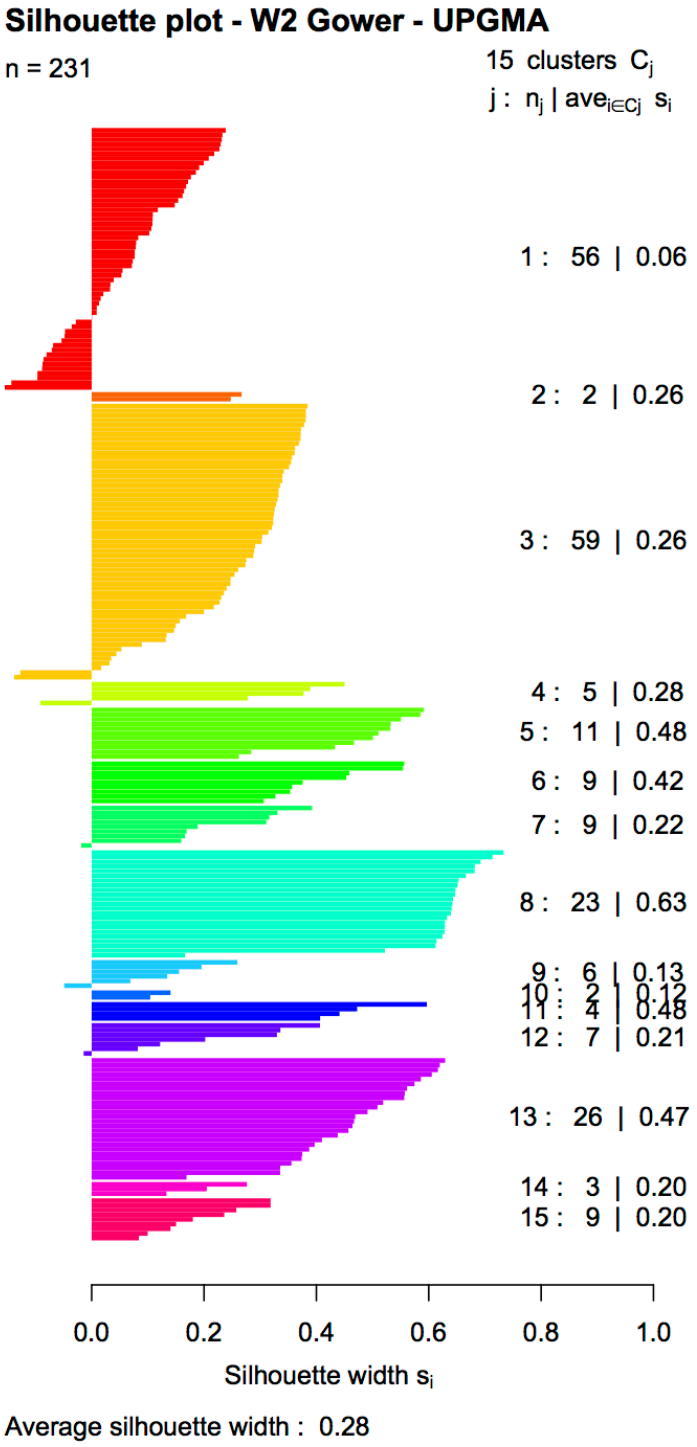


Figure 5.9 The silhouette plot of the final partition of the UPGMA dendrogram based on the W2 weighted Gower dissimilarity matrix. The group number (j), number of species per group (n_j), and average group silhouette width are shown to the right. Groups are described in-text with reference to group numbers shown here. Negative values indicated misplaced members.

The candidate emergent groups each consist of one to three genera. The silhouette width of each group is indicated in parathesis. The emergent group for the W2 weighting scheme include:

- *Cycloseris/Fungia group **CF**:* This group consists of all 23 species of the *Cycloseris* and *Fungia* genera present in Southwest Madagascar. With the W2 weighting *Cycloseris* and *Fungia* were lumped together into group 8 (*0.63*) while the W3 weighting separated the genera into two groups: Cycloseris **C** (Gr. 8, *0.51*) and Fungia **F** (Gr. 15, *0.36*). Key group traits are: maximum colony size less than 30 cm, attachment to reef-obligate freeliving, mainly solitary corals with great active sediment shedding ability, asexual reproduction occurs via fragmentation and budding from anthocaulus tissue, sometimes tissues are projected during the daytime, mainly gonochoric spawners with slow gamete extrusion, associates mainly with Clade C. Egg colour data was unavailable for all species in this group.

- *Montipora group **M**:* This group consists of all 26 species of the genus *Montipora* present in Southwest Madagascar (Gr. 13, 0.47). Key traits for this groups are: poor active sediment shedding ability, extratentacular budding, small calice size, high plasticity in corallite spacing, short tentacles that are sometimes extended by day, pink and tan coloured eggs, susceptible to bleaching but recovers quickly from bleaching episodes, not susceptible to disease, symbionts present in larva, symbiont associations with clade C and D. Some species in this group can reproduce via asexual fragmentation,

- *Pocilloporidae groups **S:*** This group consists of ten species from three genera of the *Pocilloporidae* family: *Pocillopora (P. indiania, P. damicornis, P. verrucosa, P. eydouxi)*, *Seriatopora* (*S. hysterix, S. guttatus, S caliendrum*) and *Stylophora (S. subseriata, S. pistillata, S. wellsi)*. *Acropora roseni* was also present in this group but had a comparatively narrow silhouette width (*0.28*) and was therefore dropped. This group was present with the W2 weighting (Gr. 5, *0.48*) but was combined with *Isopora* and non-hardy *Acropora* when the W3 weighting was used (Gr. 3) although the silhouette

width of this group was narrow (*0.18*) indicating weak group coherence. Key traits for this group include: extratentacular budding, determinate growth, small plocoid or subplocoid corallites, tentacles sometimes expanded by day, not susceptible to bleaching, hermaphroditic brooder and spawners with slow gamete extrusion, symbionts are present in larvae, small maximum colony size, low morphological plasticity, tentacles less than ten mm long, and each member associates with two or three symbiont clades simultaneously (combinations of A through C).

- *Porites group **P***: This group consists of nine species from the genus *Porites* and was present with both the W2 (Gr 15, *0.2*) and W3 (Gr. 6, *0.35*) weighting schemes. Key traits for this group include: poor active sediment shedding, extratentacular budding, crowded small ceroid corallites, mainly determinate growth, no tissue expansion by day, med-high bleaching resistance, high susceptibility to disease, mainly gonochoric spawners with symbionts in larvae, variable polyp colour patterns, tentacles less than 10 mm long and associates only with symbiont clade C.

- *Acropora group **A**:* This group is the largest group consisting of 59 species and was present with the W2 weighting (Gr. 3, *0.26*) but with the W3 weighting it was split into hardy-*Acropora* (Gr. 4, *0.32*) and non-hardy *Acropora* (Gr. 3, *0.18*) the latter was combined with the *Isopora* and *Pocilloporidae* group, however this group has poor coherence and is not likely to be a true emergent group. Key traits for this group were: small plocoid corallites, determinate, semi-determinate, and/or indeterminate growth, high plasticity in both colony and corallite spacing, no tissue expansion by day, cream, orange, pink, red, and white coloured eggs, no symbionts in larvae, symbiont associations with clades A, C, and D. Within this group there is a clear split in terms of hardiness with 35 species susceptible to bleaching and disease, not resistant to disease or predation and recover quickly from bleaching. Ten species are susceptible to bleaching, disease, and predation and do not recover quickly from bleaching. Finally, 14 species are neither resistant nor susceptible to bleaching, disease or predation and do not recover quickly from bleaching.

- *Isopora group **I**:* This group contains two *Isopora* species (*A. palifera*, and *A. cuneata*) and also two highly fused *Acropora* species (*A. natalensis* and *A. pinguis*). *Montipora kelllyi* was likely misplaced in this group (*-0.09*). This group is closely related to the *Acropora* group described earlier but has been separated from this group on the basis of associating only with clades C and D, and also because it contains the only brooding Acropora species (*Isopora*). This group was present with the W2 weighting (Gr. 4, *0.28*) but with the W3 weighting it was combined with the *Pocilloporidae* and non-hardy *Acropora* group (Gr. 3, *0.18*) although this group has poor coherence and is unlikely to be a true emergent group.

- *Free living colonies **H***: This group consists of four freeliving colonial species (*Halomitra pileus, Herpolitha limax*, *Herpolitha weberi*, and *Polyphyllia talpina*). This group was present using both the W2 (Gr. 11, *0.48*) and W3 (Gr. 12, *0.26*) weighting scheme, Additional key traits for this group are: asexual reproduction via budding from anthocaulus tissue and fragmentation, determinate growth, association with symbiont clade C, gonochoric spawning, dull polyp colouration, no symbionts in larvae, not susceptible to disease or bleaching, not resistant to bleaching (with the exception of *Herpolitha limax)*, does not recover quickly from bleaching. No sediment shedding or egg colour data was available for this group.

- *Bubble coral group **B***: This group contains only two species: *Physogyra lichtensteini* and *Plerogyra sinuosa.* With the W2 weighting *Symphyllia agaricia* was included in this group (Gr. 14) but had a narrow silhouette width *(0.13)* indicating misplacement. The W3 weighting excluded *S. agaricia* (Gr. 15, *0.*39). Key traits for this group include: incomplete intra-tentacular budding, meandroid and flabello meandroid corallite form, wide valleys, determinate growth, massive colony morphology, vesicles and tentacles expanded by day with daytime tissue projection greater than 20 mm, gonochoric spawning, uniform dull polyp colouration, tentacle length greater than 20 mm, associates with both symbiont clade C and D, larval symbionts are not present in larvae, neither resistant or susceptible to bleaching, disease,

or predation, and does not recover quickly from bleaching. Egg colour, spawning behaviour, and sediment shedding ability data were unavailable for this group, however, active sediment shedding ability is likely to be high for this group as it can inflate its vesicles and tentacles thereby 'shaking' off sediment. This group is often found on sediment rich reefs.

- *Agariicidae group* ***AG:*** This group initially contained 13 species but four were dropped due to narrow or negative silhouette widths *(Gardinoseris planulata, Pavona venosa, Podabacia crustacea, Galaxea astreata)*. The remaining 9 species were all from the family *Agariciidae*: including five *Pavona* species (P. cactus, P. clavus, P. decussata, P. duerdeni, P. varians), three *Leptoseris* species (*L. incrustance, L. mycetoseroides, L. yabei*), and *Pachyseris speciosa*. With the W2 weighting this group was split into Gr 9. (0.13) and Gr. 12 (0.21). With the W3 weighting these two groups combined into a more coherent group (Gr. 11, *0.32*), which became more coherent once the three outlier species were dropped (*0.36*). The key traits for this group are: thamnasteroid corallite form and budding (except *Pachyseris speciosa*), small corallite size with tentacles less than ten mm, no tissue expansion by day, determinate and indeterminate growth, foliose or laminar colony morphology, uniform dull polyp colouration, associates with clade C and D, overall not resistant to bleaching and disease, overall not susceptible to bleaching, disease, and predation, does not recover quickly from bleaching, gonochoric spawners with yellow eggs.

- *Laminar group* ***LA:*** This group contains eight species from three families including: *Pectinidae* (*Echinophyllia aspera, Mycedium elephantus, Mycedium mancaoi, Oxypora lacera*), Favidae (*Echinopora gemmacea, Echinopora lamellosa*) and Dendrophyllidae (*Turbinaria irregularis, Turbinaria mesenterina*). *Coscinarea columna* was dropped due to a negative silhouette width (*-0.02*), which increased group coherence from *0.22* to *0.25*. Using the W2 weighting the two *Turbinaria* species also had relatively low silhouette widths (*0.17*) and removing these increased average group coherence to *0.28*. This group was only present when emphasis was placed on rare traits (W2 weighting) and the W3 weighting caused it to split into Gr 1,

Gr 4, and Gr 9. Key traits for this group are: central corallite present, encrusting or laminar colony morphology, indeterminate and semi-determinate growth, can form extensive stands, high colony morphology plasticity, plocoid or scattered corallite form, intra and extra tentacular budding, high plasticity in corallite spacing, tissue not expanded by day, tentacle length ten to 20 mm or less than ten mm, not resistant to bleaching or disease, not susceptible to bleaching, disease, and predation, does not recover quickly from bleaching, hermaphroditic spawners with grey-brown, pink, and yellow egg colour, symbionts are not present in larvae, uniform dull or centre bright polyp colour pattern, associates with Clade C and D.

- *Goniopora/Alveopora group **G**:* This group contains nine species from the genus *Alveopora* and *Goniopora*. This group was present with both the W2 (Gr. 6, *0.42*) and W3 (Gr. 5, *0.48*) weighting. Key traits for this group include: high active sediment shedding ability, daytime tissue projection of 5 to 20 mm or greater than 20 mm, brown eggs, resistant to disease, but susceptible to bleaching, symbionts present in larvae, and long tentacles (ten to 20 mm).

5.3.2. Emergent groups-equally weighted major trait categories (W3)

The resulting heat map (Figure 5.10) and silhouette widths (Figure 5.11) for the W3 weighted Gower dissimilarity matrix largely showed the same groupings present with the W2 weighting scheme. There were however a number of differences: 1) *Cycloseris* and *Fungia* were separated into two groups, 2) the *Pocilloporidae* group, *Isopora* group, and non-hardy *Acropora* species were combined into one group although coherence was low (0.18), 3) a new *Leptastrea/Siderastrea* group **L** (Gr. 8, *0.48*) and 4) a fleshy dome group **FD** (Gr. 2, *0.35*) were sifted out from W2 group 1 (*0.06*). The differences in group membership resulting from the W2 and W3 weighting scheme is summarized in a contingency table (Table 5.6).

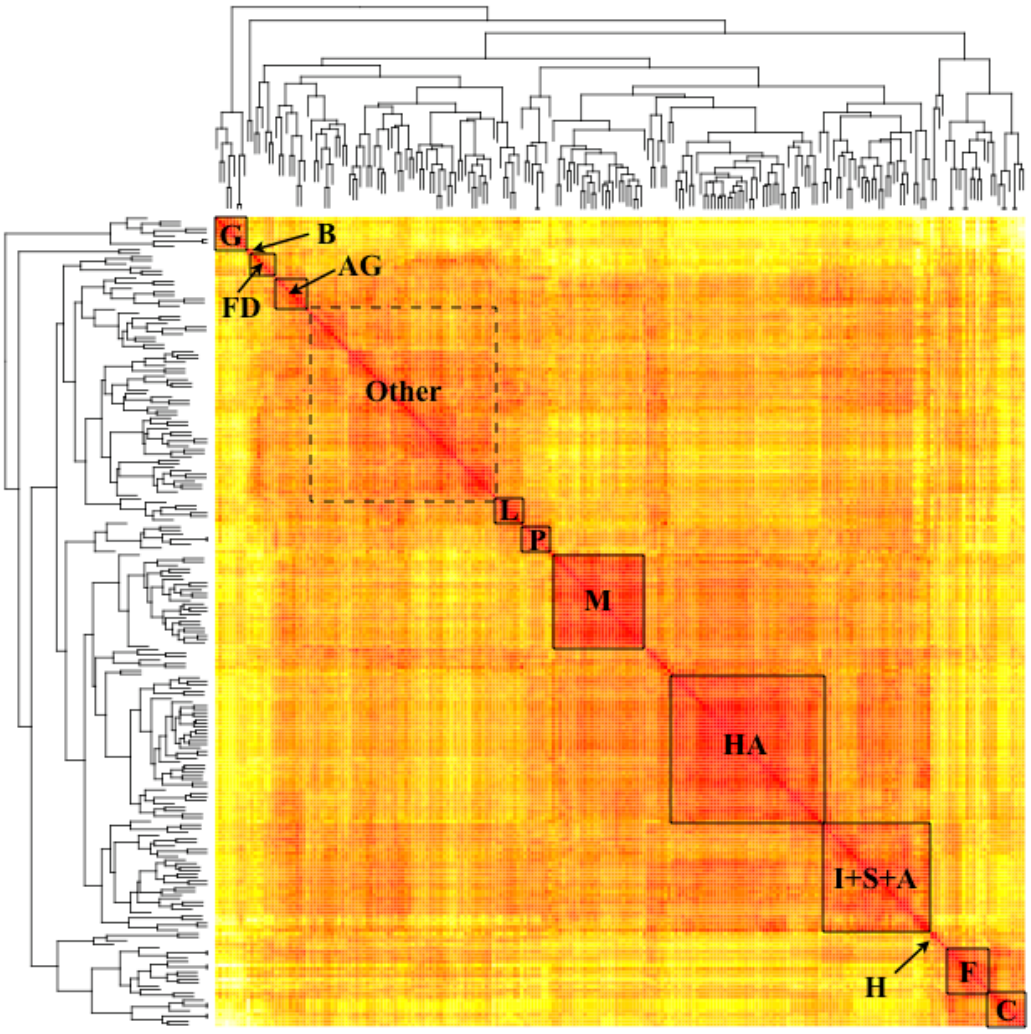


Figure 5.10 W3 weighted Gower dissimilarity matrix for the 231 species in Southwest Madagascar reordered by the dendrogram resulting from the UPGMA clustering. Red area areas indicate groups of species with high trait similarity. The labels refer to the emergent groups described in-text.

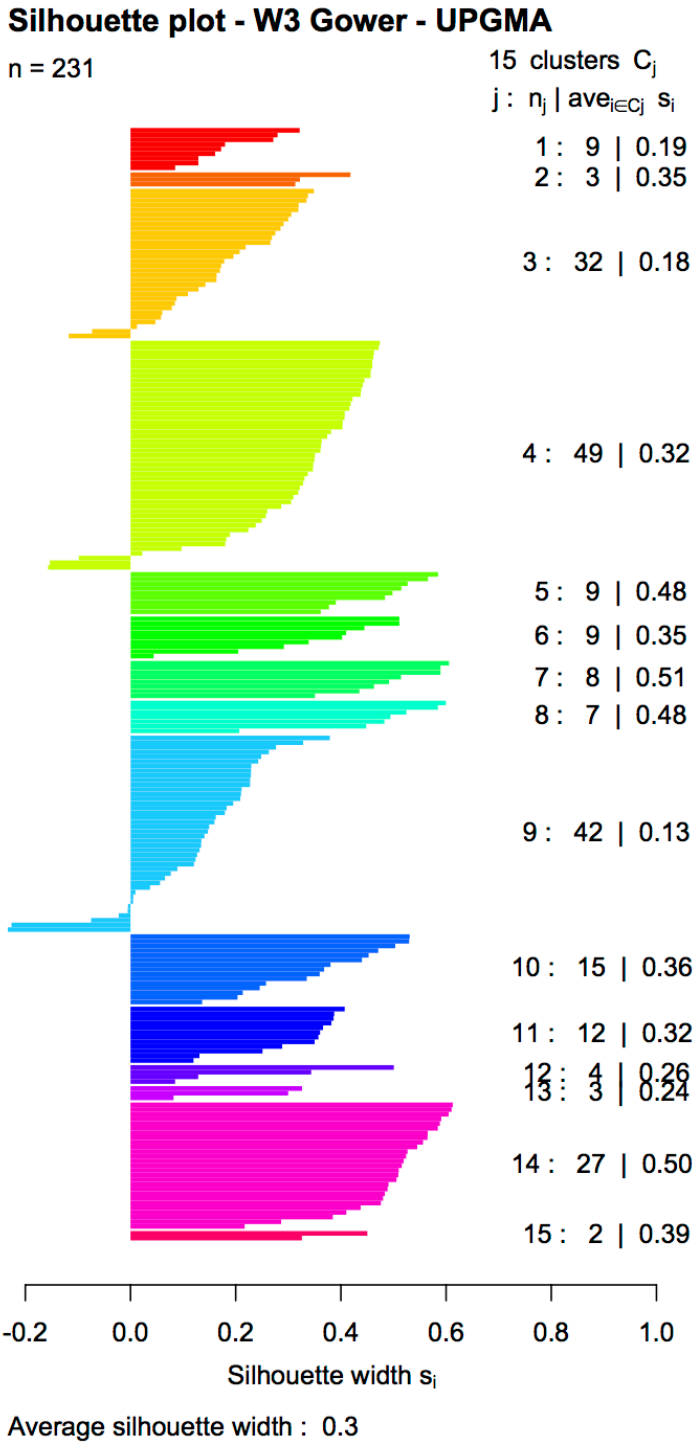


Figure 5.11 The silhouette plot of the final partition of the UPGMA dendrogram based on the W3 weighted Gower dissimilarity matrix. The group number (j), number of species per group (n_j), and average group silhouette width are shown to the right. Groups are described in-text with reference to group numbers shown here.

Table 5.6 Contingency table of groups resulting from W2 and W3 weighting scheme.

Group no.		Major trait categories weighted equally (W3)															No. of species	Silhouette width	Group members
		7	14	5	8	15	10	2	6	4	11	12	13	1	3	9			
All traits weighted equally (W2)	8	8					15										23	0.63	Cycloseris and Fungia (CF)
	5														11		11	0.48	Pocilloporidae group (S)
	11											4					4	0.48	Freeliving colonies (H)
	13		26														26	0.47	Montipora (M)
	4														5		5	0.28	Isopora type group (I)
	2							1					1				2	0.26	Acanthastrea, Lobophyllia (FD)
	3									43					16		59	0.26	All Acropora (A)
	7									1				3		5	9	0.22	Echinopora, Echinophyllia, Mycedium, Oxypora, Turbinaria (LA)
	12		1								5					1	7	0.21	Leptoseris, Pavona, Psammocora (AG)
	14					2							1				3	0.2	Physogyra, Plerogyra, Symphyllia (B)
	15								8					1			9	0.2	Porites (P)
	6			9													9	0.13	Goniopora, Alveopora (G)
	9										5			1			6	0.13	Pavona , Pachyseris (AG)
	10															2	2	0.12	Other
	1*				7			2	1	5	2		1	4		34	56	0.06	Other
No. of species		8	27	9	7	2	15	3	9	49	12	4	3	9	32	42	231		
Silhouette width		0.51	0.5	0.48	0.48	0.39	0.36	0.35	0.35	0.32	0.32	0.26	0.24	0.19	0.18	0.13			
Group members		Cycloseris (C)	Montipora (M)	Goniopora, Alveopora (G)	Leptastrea, Siderastrea (L)	Physogyra, Plerogyra (B)	Fungia (F)	Acanthastrea, Blastomussa, Plesiastrea (FD)	Porites (P)	Hardy Acropora (HA)	Leptoseris, Pavona (AG)	Freeliving colonies (H)	Lobophyllia, Symphyllia (FD)	Other	Isopora, Pocilloporidae, Non-hardy Acropora (I+S+A)	Other			

A few groups only became obvious when rare traits were de-emphasized with the W3 weighting scheme:

- *Fleshy domes* ***FD:*** This group consists of 6 species from 5 different genera: *Blastomussa merleti, Plesiastrea versipora, Symphyllia recta, Acanthastrea ishigakiensis, Lobophyllia,* and *Symphyllia agaricia*. With the W2 weighting only *A. ishigakiensis* and *L. hemprichii* grouped (Gr. 2, *0.26*). With the W3 weighting *B. merleti, P. versipora, A, ishingakiensis* grouped together (Gr. 2, 0.36) and *S. recta, S. agaricia*, and *L. hemprichii* grouped together (Gr. 13, 0.23). These two groups were closely related according to the dendrogram and are considered here as one emergent group. Key traits for this groups are: strong sediment shedding ability, valley widths of 5 to 15 mm or greater than 15 mm, determinate growth, massive or submassive colony morphology, crowded corallite spacing, daytime tissue projection of 5 to 20 mm, most can have either mantles or tentacles expanded by day, tentacle length of 10 to 20 mm, tan egg colour, not resistant to bleaching or disease, not susceptible to bleaching, disease, or predation, does not recover quickly from bleaching, gonochoric or hermaphroditic spawner with vigorous gamete ejection and no symbionts in larvae, low plasticity in colony morphology, high plasticity in polyp colour patterns, associates with symbiont clade B-D. Corallite form was quite variable for this group (ceroid, flabello-meandroid, meandroid, phaceloid, and subplocoid or sub ceroid).

- *Leptastrea group* ***L****:* This group consisted of six species and contained both the family *Faviidae* (*Leptastrea aequalis, Leptastrea bottae, Leptastrea purpurea, Leptastrea transversa, Goniastrea peresi*) and *Siderastreidae* (*Siderastrea savignyana*). *Diploastrea heliopora* was dropped from this group as it had a comparatively narrow silhouette width (0.21). This exclusion increased the average silhouette width from *0.48* to *0.52*. Key traits for this group are: extratentacular budding, corallites one to five mm or five to 15 mm, determinate growth, encrusting and submassive growth forms, ceroid or plocoid, crowded corallite spacing, no tissue expansion by day, not resistant to bleaching or disease, not susceptible to bleaching, disease, or predations, does not recover quickly from bleaching, gonochoric spawning

with no symbionts present in larvae, max 50 cm to one m in colony diameter, walls of polyps brightly coloured, associates only with clade C, and short tentacles (less than 10 mm). Egg colour was not available for this group.

5.4. Discussion

Between the two weighting schemes 13 emergent groups could be identified and these are summarized in Table 5.7 below.

Table 5.7 Emergent groups in Southwest Madagascar

Code	Group	No. Species
CF	*Cycloseris/Fungia*	23
M	*Montipora*	26
S	*Pocilloporidae*	10
P	*Porites*	9
A	*Acropora*	59
I	*Isopora*	4
H	Free-living colonies	4
B	Bubble coral	2
AG	*Agariicidae*	9
LA	*Laminar*	8
G	*Goniopora/Alveopora*	9
FD	Fleshy domes	6
L	*Leptastrea*	6
-	Other	56
	Total	231

Most of the groups were present when using both the W2 and W3 weighting scheme, increasing confidence that these are true emergent groups and not simply artefacts of any particular weighting scheme or that the weighting schemes might be masking potential groupings.

Regardless of weighting scheme used, 56 species did not fit neatly into groups (see 'other' block in Figure 5.8 and Figure 5.10) indicating that these corals have unique trait combinations. This makes clear that the use of emergent groups alone is not sufficient for examining the trait diversity of coral reefs at least in Southwest Madagascar and probably elsewhere as well. What is needed is the development of a

hybrid approach that combines emergent groups and individual species (this approach is developed in subsequent chapters).

In a way this is fortunate because species in some emergent groups, especially in the *Acroporidae* family, are difficult to tell apart underwater. Treating these species as emergent groups of functionally redundant species is more feasible than trying to identify each to species level.

Please note that species within emergent groups can only be considered functionally redundant for the traits tested; they may be different in terms of traits not included here such as aggressive ability.

6.
Trait vs. Species Site Similarity

6.1. Introduction

Fundamental to any multivariate analysis is establishing an appropriate definition of resemblance between sample pairs. What is meant by 'similar' depends on both the context and the purpose of the analysis. The number of similarity measures available are extensive and well described (see for example Legendre and Legendre, 1998).

One of the most fundamental measures of similarity is that of Renkonen (1938):

$$S_p = \sum_{i=1}^{S} \min (p_{i1}, p_{i2})$$

where p_{i1} denotes the relative abundance of species *i* at site one and p_{i2} denotes the relative abundance of species *i* at site two. The *Renkonen* similarity measure is simply the *overlap* in terms of species relative abundance between two sites. For species composition data S_p ranges from 0 (complete dissimilarity) to 1 (complete similarity), and most similarity measures include a term representing the species overlap (i.e. *Bray-Curtis, Sørensen, Jaccard*).

While such measures are useful they are harshly absolute; different species are considered completely dissimilar while in reality some pairs of species are very similar in terms of their morphology, physiology, and behaviour while others are not.

In this chapter, using the dataset from Southwest Madagascar I:

1. Introduce a novel trait-similarity measure (hereafter *Tsim*)
2. Demonstrate how species similarity measures such as the *Renkonen* fail to identify important functional similarities between reef communities
3. Highlight the importance of supplementing species similarity measures with trait-based measures such *Tsim.*

6.2. The Trait similarity measure (*Tsim*)

Traditional similarity measures quantify the overlap of species composition between two sites. The 'remainder', i.e. the unique species composition at each site in the site pair is considered to represent dissimilarity. This approach to determining similarity between communities ignores the point that some species are highly similar in terms of life-history traits and therefore functionally similar, while others are not.

For example, three shallow reefs (*Reef A - C*) with the following species compositions: *Reef A)* 100 percent branching *Acropora* species *Reef B)* 50 percent branching *Montipora* species and 50 percent *Porites* species and finally *Reef C)* 50 percent *Fungia* and 50 percent *Cycloseris* species. With current knowledge, one may say that *Reef A* and *B* are highly functionally *similar* in terms of life-history traits while *Reef* C is highly functionally *dissimilar* to both *Reef A* and *Reef* B. Despite this, because there is no overlap of species between any of the sites, a species-based similarity measure would indicate that that all sites were equally similar or dissimilar.

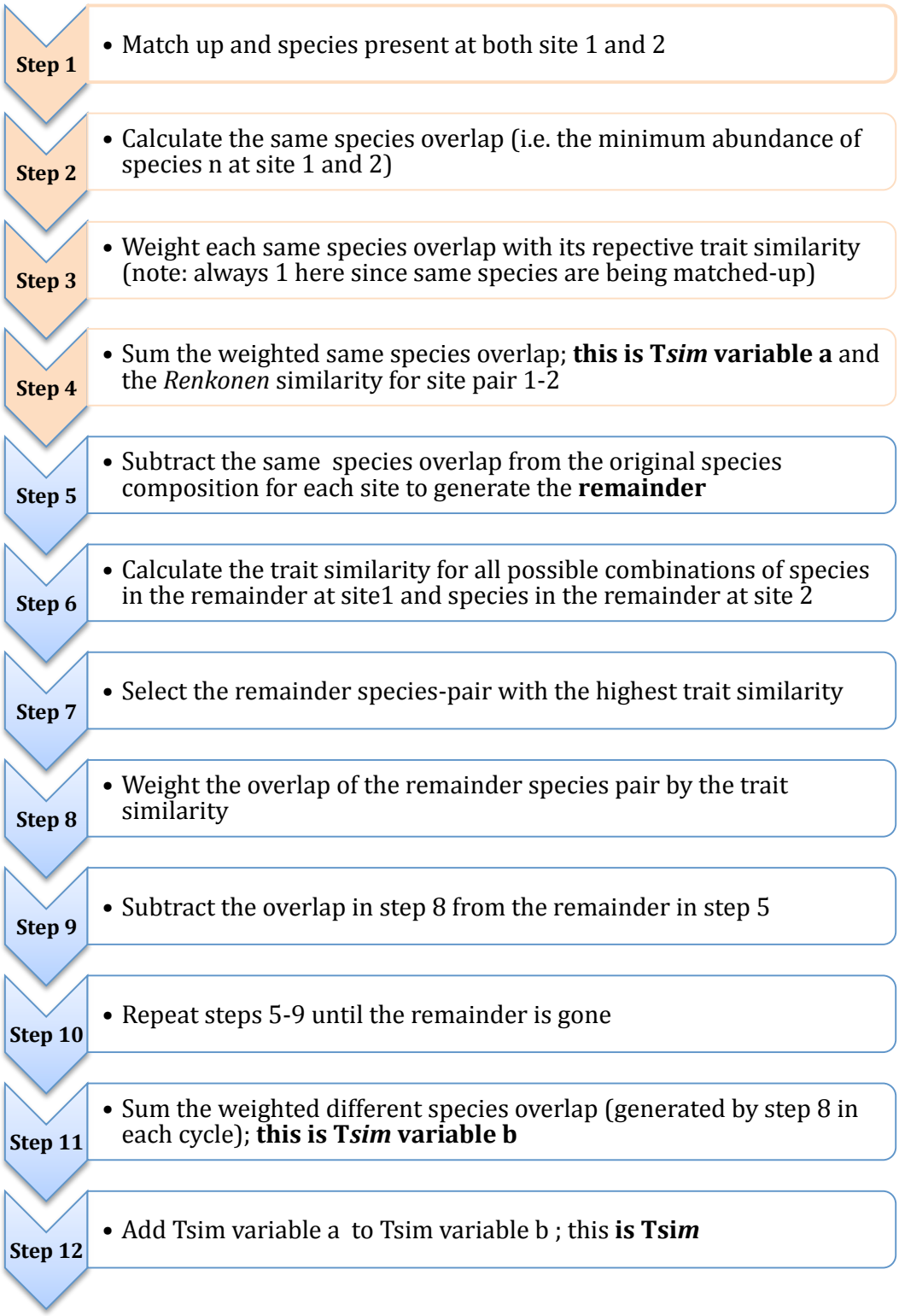
Therefore it is important to supplement measures of species overlap with one that considers the similarity of the remainder as well. Whilst it may be tempting to translate species composition directly into trait composition (by multiplying a site-species matrix by a species-trait matrix thereby producing a site-trait matrix) this is inappropriate because traits are 'packaged' within the species unit and cannot be considered as independent entities. Traits pass through environmental filtering events (such as warming events) in particular combinations, while species pass through such a filter individually.

To respect that traits occur in fixed combinations within a species one must calculate the trait similarity between sites without 'removing' the traits from the unit of the species. This can be done by calculating how similar the species in each 'remainder' are in terms of their trait combinations using Gower's general coefficient of similarity (Gower, 1971). The Gower similarity between species pairs ranges from 0 to 1 and increases as their trait combinations become more similar.

Here I present a new similarity measure, *Tsim*, which first calculates the overlap in species composition between two sites (which can also be viewed as the overlap in identical trait combinations) and then compares how similar the species composition is of the 'remainders' (i.e. non-overlapping species composition) in terms of their trait combinations. It does so by using the Gower similarity to define the trait similarity between species pairs. For clarity, the process of calculating *Tsim* is first presented schematically, then mathematically after which a simple example of its implementation is given.

6.3. Calculating *Tsim*

6.3.1. A schematic overview



6.3.2. Mathematical definition

Tsim is the sum of: a) the overlap of the species composition between site *x* and *y* b) the trait similarity between the 'remainder' at site *x* and *y* and c) the trait similarity between the 'remainder' at site *x* and *y*. The sum is then divided by the union of the two sample sites (for frequency data where the total site abundance is standardized to one, the denominator of $Tsim_{x,y}$ will always be two).

Stated mathematically for site *x* and *y* the *Tsim* similarity is then:

$$Tsim_{x,y} = \frac{2a + b + c}{2}$$

where ,

a = Σ minimum frequency for species present at site *x* and *y* (i.e. the overlap between the species composition between site *x* and *y*; commonly known as the *Renkonen* similarity)

$b = \sum x_n$ for species present at site x but not y (i.e. the similarity between the 'remainder' species composition at site *x* and the 'remainder' species composition at site *y*)

x_n = The overlap between the frequency of a species at site *x* and the species present at site *y* that has the greatest Gower similarity score for the species in question. This overlap is then weighted by the associated Gower similarity.

$c = \sum y_n$ for species present at site y but not x (i.e. the similarity between the 'remainder' species composition at site *x* and the 'remainder' species composition at site *y*)

y_n = The overlap between the frequency of a species at site *y* and the species present at site *x* that has the greatest Gower similarity score for the species in question. This overlap is then weighted by the associated Gower similarity.

Because term *b* and *c* are always equal *Tsim* can be simplified to:

$$Tsim_{x,y} = a + b$$

where *a* contains all information about species overlap (i.e. the *Renkonen* similarity) and *b* contains all information about the similarity of the 'remainder' at both sites

once the species overlap has been accounted for. $Tsim_{x,y}$ can range between null (no similarity) and one (complete similarity).

6.3.3. Simple example of calculating Tsim

For clarity, an example of how to calculate *Tsim* for two very simple hypothetical communities follows.

Site	**Species A**	**Species B**	**Species C**
x	0.2	0	0.4
y	0.1	0.3	0.3

$a = 0.1 + 0.3 = 0.4$

Subtracting *a* from the species-site matrix leaves:

Site	**Species A**	**Species B**	**Species C**
x	0.1	0	0.1
y	0	0.3	0

Site x	**Site y**	***G***
Species A	Species B	0.7
Species C	Species B	0.4

The Gower similarity (*Gsim*) is then used to calculate $x_{n.}$ Since the *Gsim* score for Species A and B is greater than the *Gsim* score for Species B and C this is considered first.

Overlap between Species A_x and Species B_y weighted by *Gsim* is then:

$0.1 \times 0.7 = 0.07$

As this weighted overlap is now accounted for it is subtracted from the species-site matrix leaving:

Site	**Species A**	**Species B**	**Species C**
x	0	0	0.1
y	0	0.2	0

Site x	**Site y**	***Gsim***
Species A	Species B	0.7
Species C	Species B	0.4

Overlap between Species C_x and B_y weighted by *Gsim* is then:

0.1 x 0.4 = 0.04

Thus,

$b = 0.07 + 0.04 = 0.11$

and ,

$Tsim_{xy} = a + b = 0.4 + 0.11 = 0.51$

The advantages of *Tsim* to traditional species similarity measures are many. Firstly, *Tsim* contains all information about species overlap given by the *Renkonen* similarity and further, unlike the Bray-Curtis it is density invariant when calculated using species composition data and can therefore be considered a valid measure of compositional species similarity. Note that *Tsim* is not density independent when using total composition data (i.e. no. of points of coral species *A* divided by total no. of points surveyed).

Secondly, since *Tsim* relies on the *Gower similarity* to determine the trait similarity between species, *Tsim* includes all benefits of the *Gower similarity* coefficient: 1) it can handle missing trait data 2) it allows for joint absences of traits to be considered important 3) it allows for weighting traits by importance or of special interest to the analyst.

Finally, and perhaps most importantly, unlike traditional species similarity indices, *Tsim* does not ignore sites that are *functionally similar* (in terms of trait combinations) despite having highly dissimilar species compositions. The terms

'functional similarity', 'trait similarity' and '*Tsim*' are hereafter used interchangeably to refer to the similarity between reef sites in terms of the 26 life-history traits used in this study. Likewise the terms 'mechanical similarity', 'species similarity', and '*Renkonen*' are used interchangeably to refer to the similarity in terms of species overlap between reef sites.

6.4. Methods: Exploratory data analysis and coding

An exploratory analysis was undertaken to gain a general impression of the data and information about simple parameters and variable distributions. Based on the observations made during the exploratory data analysis (described below) appropriate transforms were selected (a process commonly referred to as 'coding' ; Legendre and Legendre, 1998).

6.4.1. Influence of species cluster replacement on frequency distributions

The influence of the commonality weighted random replacement of species clusters (i.e. *Acropora* branching) with actual species (procedure detailed in Chapter Four) on frequency distributions was examined for each depth category (Appendix Figures 8.1 to 8.4). The replacement procedure did not change the overall shape of the frequency distribution. Replacement did obviously increase the overall number of species at each site and therefore the frequency distribution was somewhat smoother for species-only data as compared to species cluster data. Overall, comparing the frequency distribution between species data and species cluster data ensured that this step was not confounding results in later analysis.

6.4.2. Transforming the raw data frequency distributions

Acropora and *Montipora* heavily dominated species frequency distributions at each depth range (see Appendix Nine). In order to select the most appropriate transformation to down-weight the contributions of these quantitatively dominant genera to the species frequency distributions several common transforms were tested including: square root, fourth root, log transform, the log transform suggested by Andersson et al. (2006), normalization, chi-squared, and the Hellinger transform. The fourth root transform was used for all data as it maintained the structure of the data the best while de-emphasizing the dominance of *Acropora* and *Montipora* for all depth zones.

6.4.3. Standardisation of species data

The species count data was standardized to species compositional data i.e. the total coral abundance for each site was 100 percent (hereafter species composition), because *Tsim* is only density independent if species composition data is used. If data is standardized to total composition i.e. the total coral and non-coral abundance for each site is 100 percent, then *Tsim* will contain information about both trait combination similarity and total coral abundance. However, pulling apart the influence of the overall similarity in coral coverage from the influence of overlapping trait-combinations on *Tsim* is not possible. For this reason only species composition standardized data was used in the analysis.

6.5. Methods: Calculating *Tsim* and *Renkonen*

The function **Tsim( )** for calculating *Tsim* was coded in **R.** The function is annotated and available electronically in Digital Supplement 1.3. Due to the number of permutation required for calculating *Tsim* for large datasets users should be advised that calculation of *Tsim* could take considerable time.

6.6. Results: Relationship between *Tsim* and Renkonen similarity

Consider the analogy of a reef (or any ecosystem) as a machine that is comprised of mechanical parts (nuts, bolts, cogs etc.) that each have a particular functionality associated with it. While there may be many types of cogs they all inherently have the same functionality (i.e. rotation). Likewise many species have the same functionality with regard to a particular set of traits. One can therefore refer to a reef's species composition as its 'mechanical composition' and the 'trait-combination composition' (note: not trait-composition) as its 'functional composition'. Plotting *Tsim* against the *Renkonen* similarity allows for the positioning site pairs in mechanical and functional similarity space (hereafter mechano-functional space or simply 'mf-space'). Each corner of such a plot in is now explained using Figure 6.1.

Sites with dissimilar species composition and dissimilar trait combination composition are mechanically and functionally dissimilar (Corner A; Figure 6.1). Sites with similar species composition and consequently similar trait combination compositions are mechanically and functionally similar (Corner B; Figure 6.1). Sites with similar species composition and dissimilar trait combination composition would be mechanically similar but functionally dissimilar (Corner C; Figure 6.1), but in reality such site pairs cannot exist and therefore this corner of the graph is never occupied. While trait variation within a species is possible, the assumption here is that trait variations between species are always greater than within a species.

Sites with dissimilar species composition but similar trait combination composition are mechanically dissimilar but functionally equivalent (Corner D; Figure 6.1). Such site pairs are of particular interest because these site pairs are not recognized by conventional species similarity measures as being similar but are functionally similar and therefore ecologically important. Since *Tsim* can detect such important functional similarities between sites it should be used as a supplement to traditional species similarity measures.

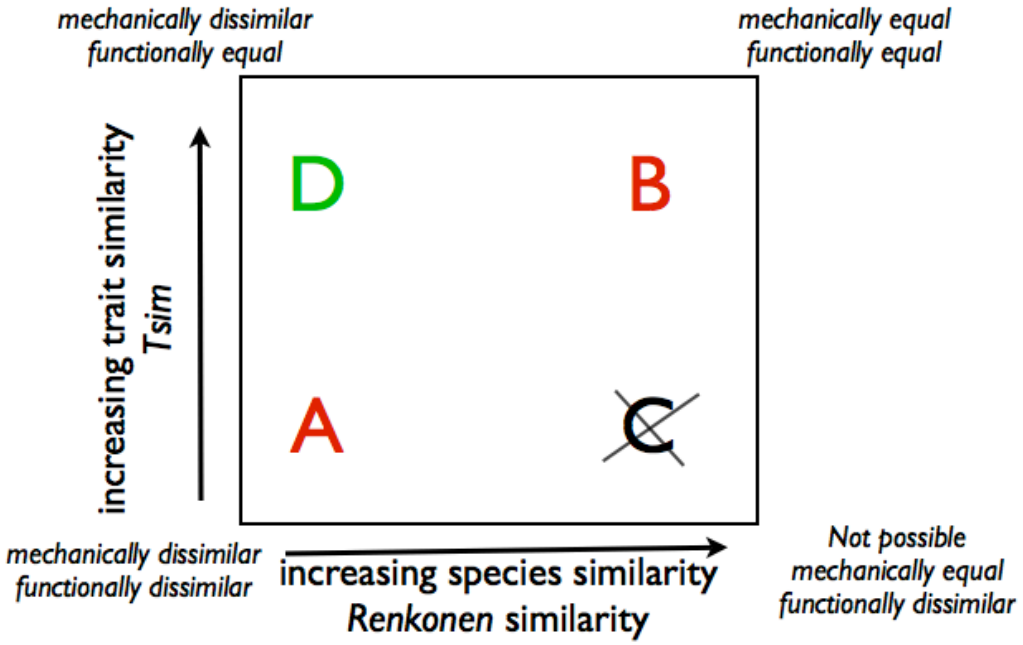


Figure 6.1 Diagram explaining what the different regions of a *Tsim* vs. *Renkonen* similarity plot represents. A) Site pairs that have no species in common and have completely dissimilar trait combination, B) site pairs with exactly the same species composition and therefore also exactly the same trait-combination composition, C) site pairs that are equal in terms of species composition will always be equal in term of trait-combination therefore this region of the graph is never occupied, D) site pairs that have no or low species composition overlap but do have high levels of trait-combination overlap, that is, they are functionally similar but mechanically dissimilar.

The *Tsim –Renkonen* plots for the four depth zones are shown below (Figure 6.2 to Figure 6.5). The models that best fitted the plot data were linear for the two to five m (r^2 = 0.6053) and eight to 15 m (r^2 = 0.6001) depth zones. A third order polynomial provided the best fit for the five to eight m (r^2 = 0.5699) and 15-26 m (r^2 = 0.6148) depth zone.

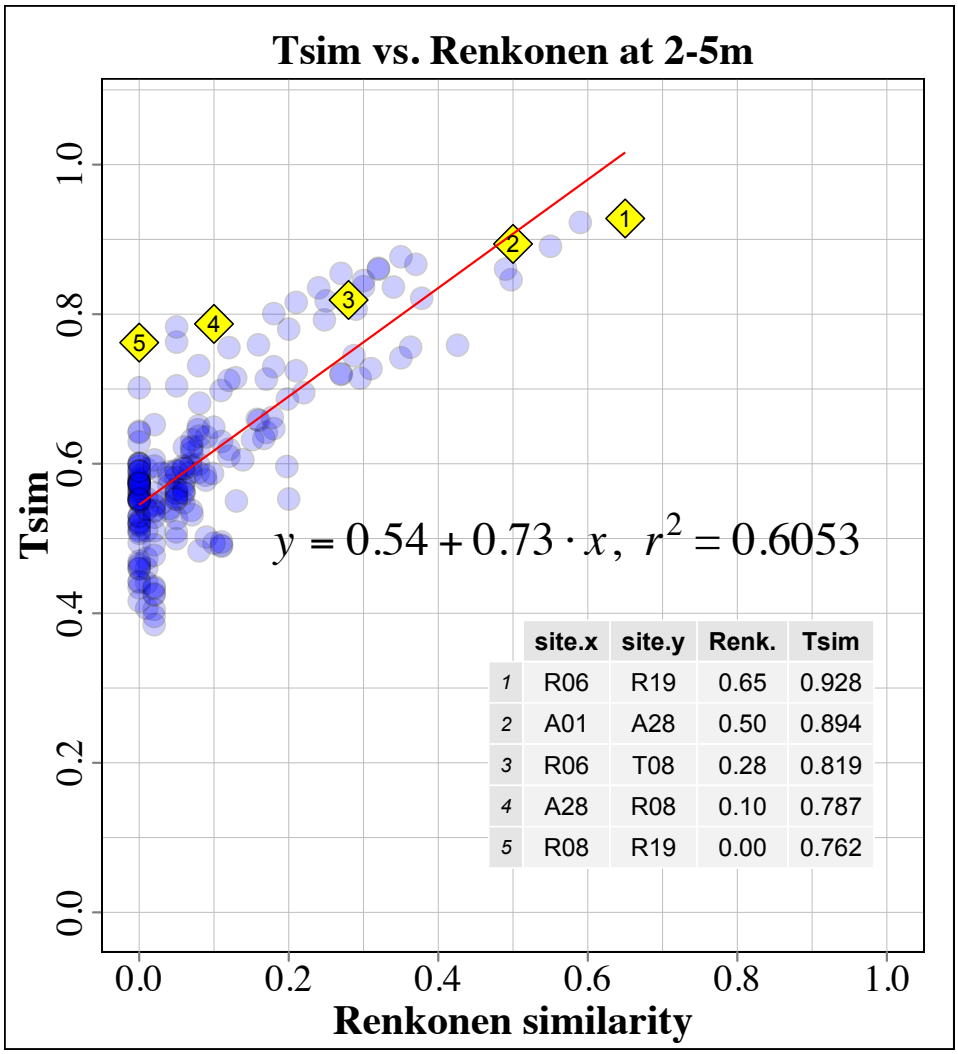


Figure 6.2 Trait combination similarity (*Tsim*) against species similarity (*Renkonen*) for site pairs at two to five metres depth (21 sites total resulting in 210 site pairs). A linear model was found to fit the best but the fit was still poor (r^2 = 0.6053) indicating that the relationship between *Tsim* and *Renkonen* can be highly variable. The distribution along the y-axis represents the variation in trait similarity for sites with the same level of species similarity. The data points are slightly transparent to allow overlapping points to be shown more clearly. The yellow diamonds labels correspond to the respective site pairs shown in the inset table. The five site pairs shown here are shown as an E-plot in Figure 6.9 and site pair A28-R08 is shown as a AWH plot in Figure 6.10.

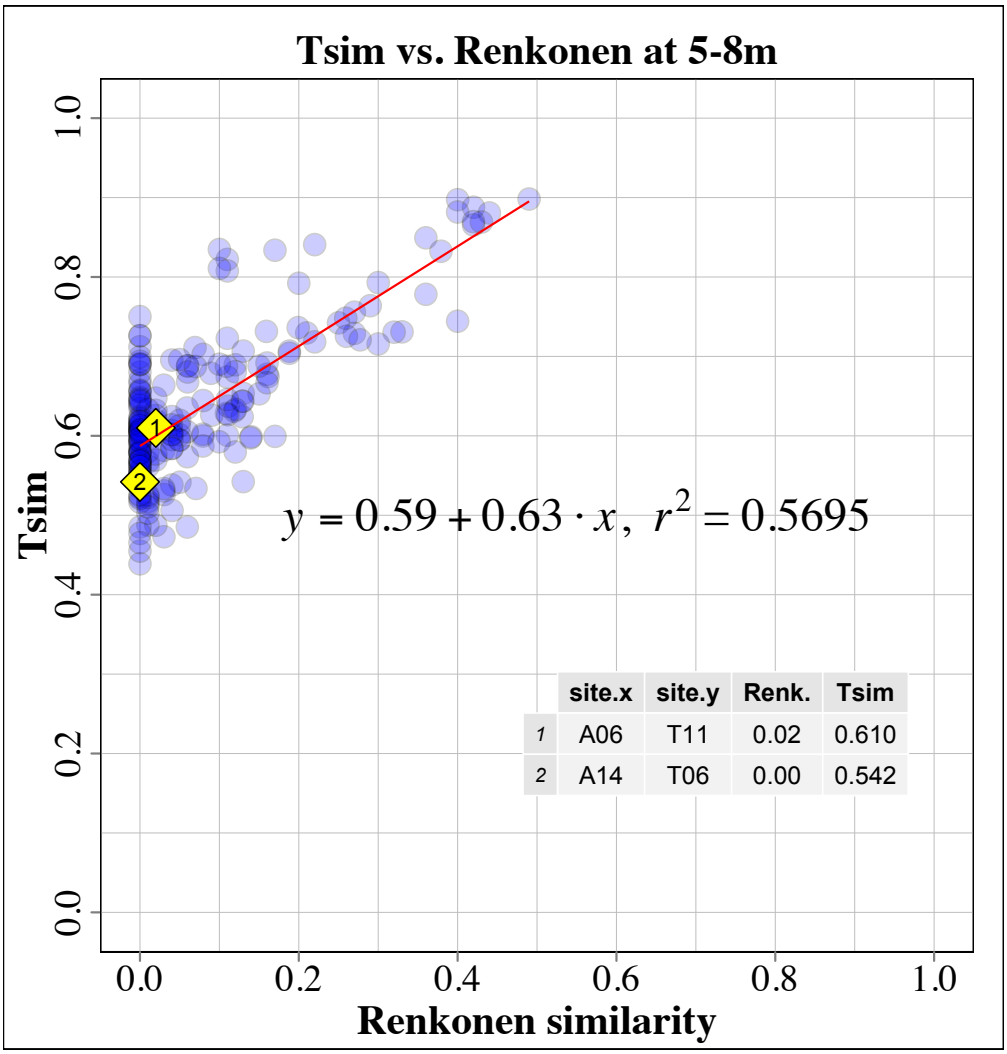


Figure 6.3 Trait combination similarity (*Tsim*) against species similarity (*Renkonen*) for site pairs at five to eight metres depth (21 sites total resulting in 210 site pairs). A 3rd order polynomial model was found to fit the best but the fit was still poor (r^2 = 0.5699) indicating that the relationship between *Tsim* and *Renkonen* can be highly variable. The distribution along the y-axis represents the variation in trait similarity for sites with the same level of species similarity. The data points are slightly transparent to allow overlapping points to be shown more clearly. The yellow diamonds labels correspond to the respective site pairs shown in the inset table. The two site pairs shown here are shown as an E-plot in Figure 6.12 and AWH plots in Figure 6.13 and Figure 6.14.

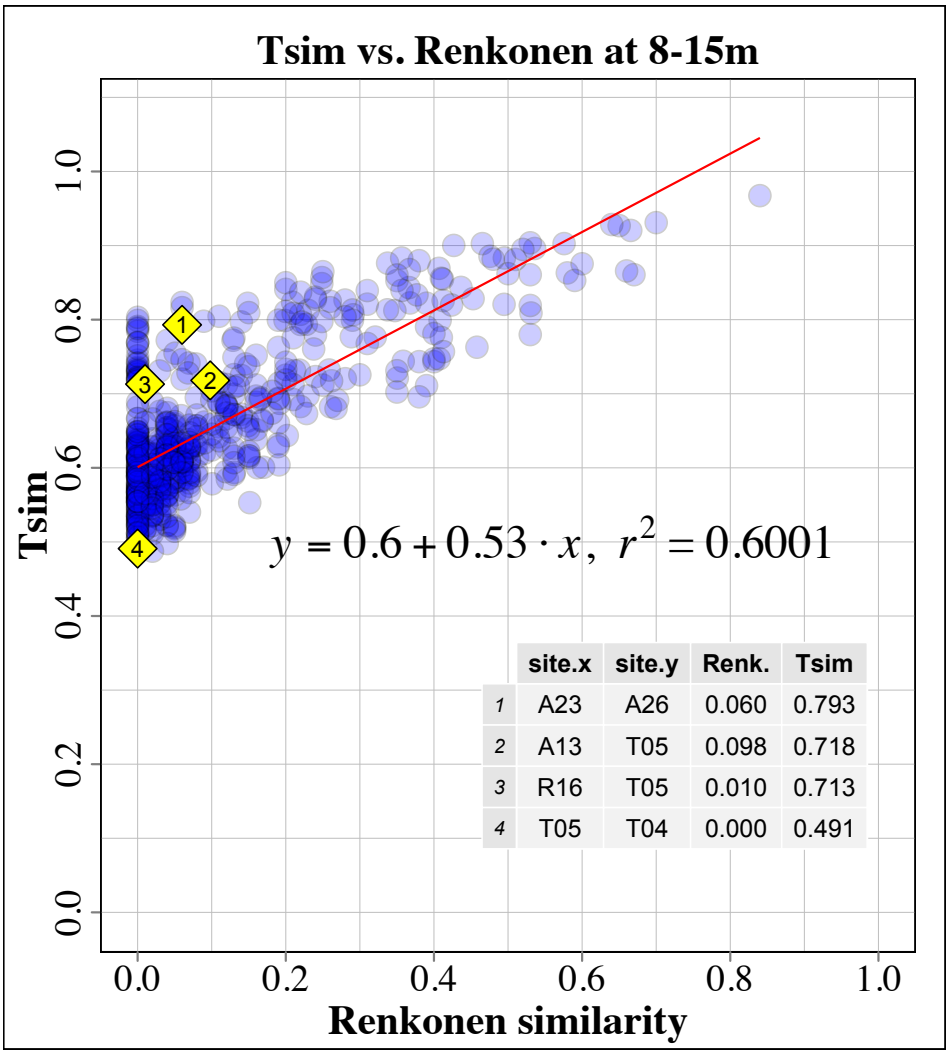


Figure 6.4 Trait combination similarity (*Tsim*) against species similarity (*Renkonen*) for site pairs at eight to 15 m depth (34 sites total resulting in 561 site pairs). A linear model was found to fit the best but the fit was still poor ($r^2 = 0.6001$) indicating that the relationship between *Tsim* and *Renkonen* can be highly variable. The distribution along the y-axis represents the variation in trait similarity for sites with the same level of species similarity. The data points are slightly transparent to allow overlapping points to be shown more clearly. The yellow diamonds labels correspond to the respective site pairs shown in the inset table. The four site pairs shown here are shown as an E-plot in Figure 6.15 and as AWH plots in Figure 6.16 to Figure 6.18 and Figure 6.20.

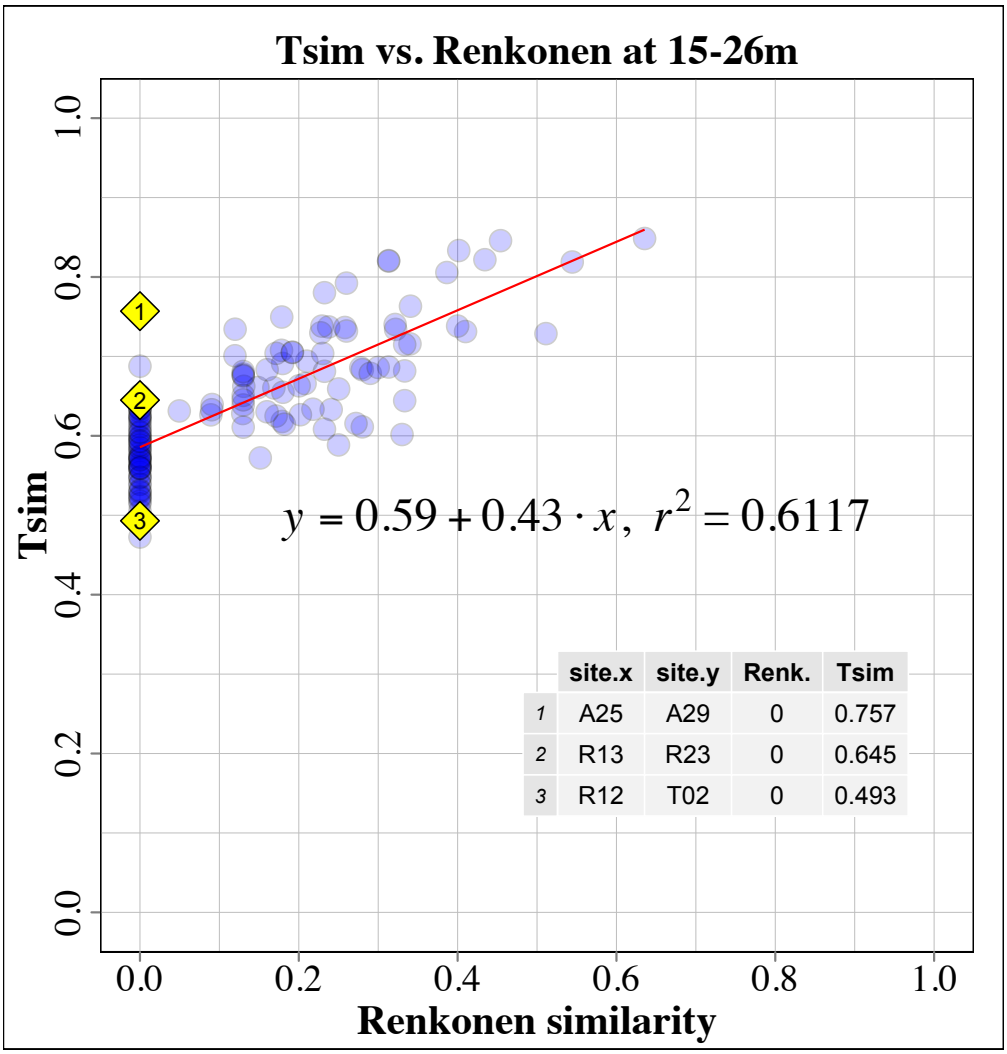


Figure 6.5 Trait combination similarity (*Tsim*) against species similarity (*Renkonen*) for site pairs at 15-26 m depth (17 sites total resulting in 136 site pairs). A 3rd order polynomial model was found to fit the best but the fit was still poor ($r^2 = 0.6148$) indicating that the relationship between *Tsim* and *Renkonen* can be highly variable The distribution along the y-axis represents the variation in trait similarity for sites with the same level of species similarity. The data points are slightly transparent to allow overlapping points to be shown more clearly. The yellow diamonds labels correspond to the respective site pairs shown in the inset table. The three site pairs are shown as an E-plot in Figure 6.21and as AWH plots in Figure 6.22 to Figure 6.24.

For all depth zones *Tsim* was highly variable against low *Renkonen* scores. That is for a given level of low mechanical similarity, functional similarity was highly variable. This variability represents important ecological information that species similarity measures fail to capture but that *Tsim* detects. In the remaining sections of this chapter specific examples are given explaining why site pairs with low species

similarity still can have high trait similarity by highlighting the species that are responsible for this trait similarity using the graphical tools described in the following section.

The environmental forcing factors that may be bringing about trait similarity between sites is eluded to were appropriate in this chapter but is discussed detail in Chapter Nine.

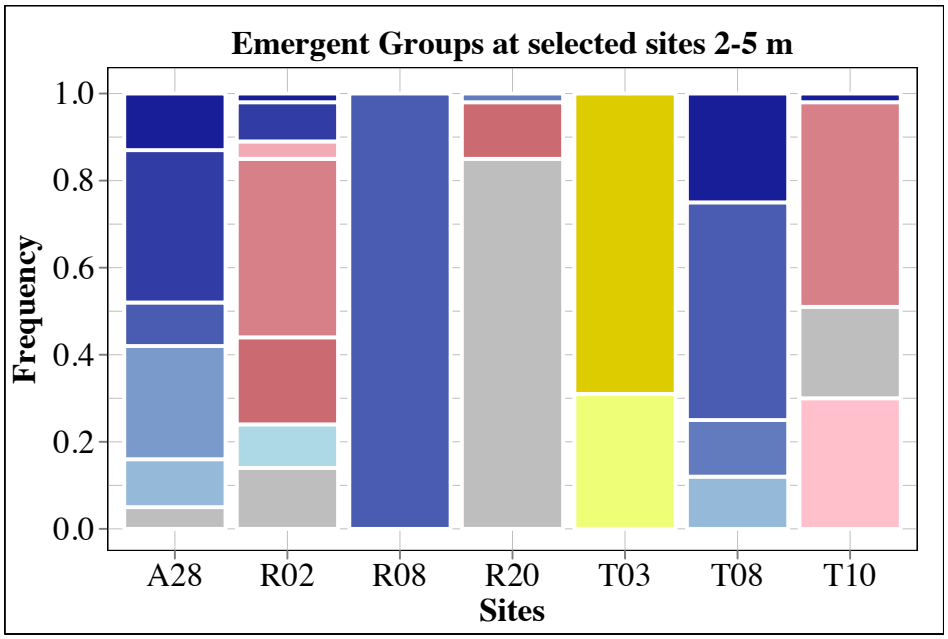
6.7. Results: Data visualization tools

6.7.1. Data visualization tools

In order to explore the major trends of site pair positioning in the mechano-functional space (i.e. Figure 6.2 to Figure 6.5) two data visualization tools were developed using R (script available in Appendix Eight). Before presenting the finding these tools allowed for, both graphical tools are briefly explained.

6.7.1.1. E-plots

The first graphical tool is called an 'E-plot' or Emergent plot. This tool allows the user to specify a region of the mechano-functional space using a maximum and minimum *Tsim* and *Renkonen* similarity values and also the number of site pairs to be displayed. The E-plots then displays the emergent group composition and the *Tsim/Renkonen* scores for the number of site pairs and plot region specified. The site pairs that have the highest *Tsim* scores relative to their Renkonen scores are displayed. In other words, an E-plot displays the site pairs that are the most functionally similar but mechanically different for a specified region. An example of an E-plot is shown below (Figure 6.6).



Emergent Groups
- Acropora.bushy
- Acropora.corymbose
- Acropora.digitate
- Acropora.staghorn
- Acropora.tables.and.plates
- Agariicidae
- Cycloseris.Fungia
- Fleshy.Domes
- Isopora
- Montipora
- Other
- Pocilloporidae
- Porites
- Porites.massive

	site.x	site.y	Renk.	Tsim
1	R02	T03	0.00	0.443
2	R20	T10	0.00	0.441
3	A28	T10	0.01	0.441
4	T08	T10	0.02	0.436
5	R08	T10	0.00	0.434

Figure 6.6 Example of an Emergent plot or 'E-plot' of the emergent group composition for a user specified region of a *Tsim-Renkonen* plot (see Figure 6.2) and number of site pairs (here five are selected). The R script for the E-plot function is available in Digital Supplement 1.3.

As discussed and presented in Chapter Six, an emergent group is a group of species that 'emerge' in trait space due to having similar combinations of life history traits. The similarity in terms of trait combinations between each species pair was determined using *Gower similarity*. Note that all species within an emergent group are not equally similar or dissimilar to one another and likewise all emergent groups

are not equally similar or dissimilar to one another. Also, note that the emergent groups play no role in the computation of either *Tsim* or the *Renkonen* similarity but are merely being used as a tool to show major trends between sites in terms of trait similarity.

The trait similarity relationships both within and between emergent groups are visible in the following trait similarity heat map (Figure 6.7; note this is not an E-plot). E-plots divide the emergent groups *Montipora* and *Acropora* into their respective species clusters (defined in Chapter Seven) for added detail.

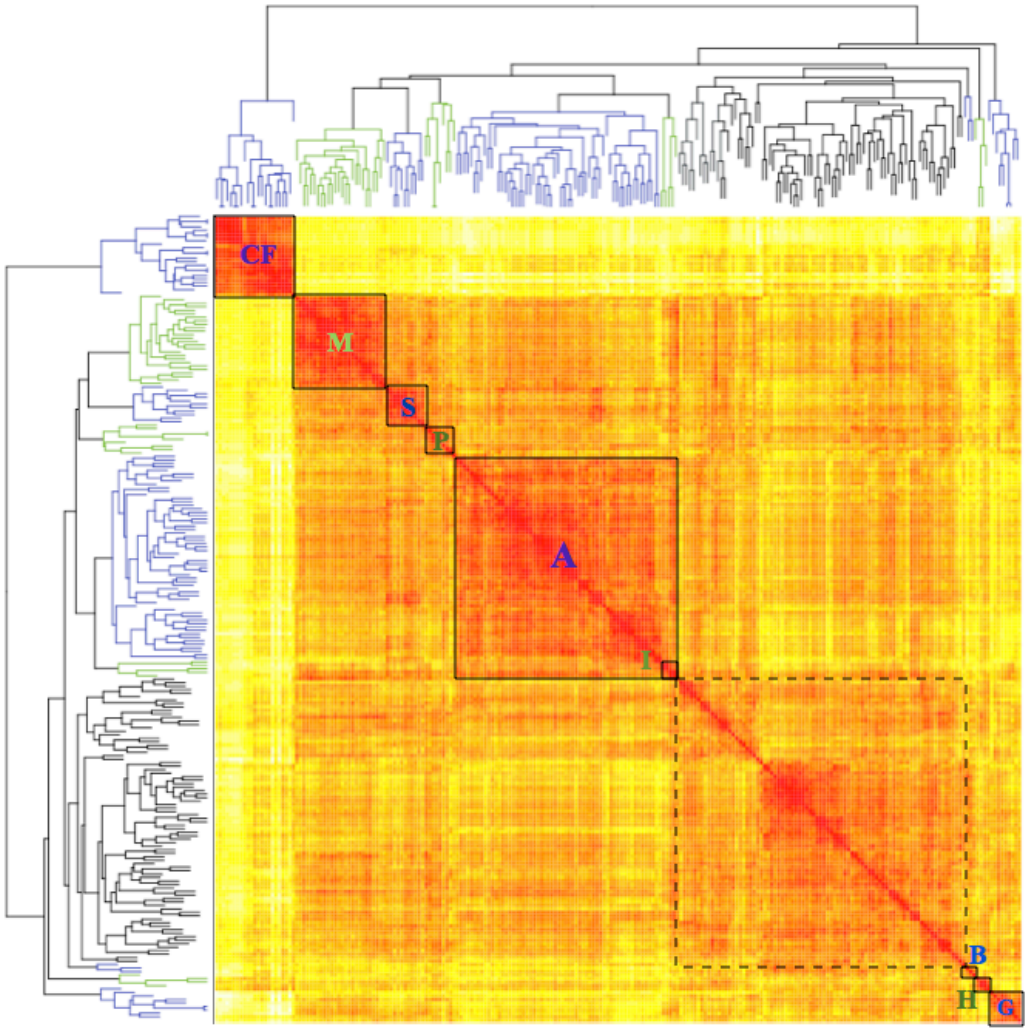


Figure 6.7 Heat map of emergent groups from Chapter Six showing how closely the emergent groups are related to one another. The labels are as follows: CF- *Cycloseris* and *Fungia*, M- *Montipora*, S-*Pocilloporidae*, P-*Porites*, A-*Acropora*, I-*Isopora*, B-Bubble coral, H-Free-living colonies, G- *Goniopora*/*Alveopora*. The box in dashed lines show the group referred to as 'other'. This contains species that do not form identifiable groups but rather exhibits a gradient of trait combinations. Emergent groups are used in this chapter to describe the behaviour of *Tsim*. The axes of the heatmap show the dendrogram resulting from clustering based on *Gower* similarity between species (see Chapter Six for more detail).

6.7.1.2. Abundance weighted heat-plot

The second graphical tool developed is an 'abundance weighted heat plot' or AWH-plot. Here the user specifies a site pair of interest and the species compositions of the two sites are plotted against one another such that the size of each 'overlap box' represents the percentage in overlap between species pairs between sites. The overlap boxes are then coloured using the Gower similarity score for the species-pair, which shows the level of trait similarity between the two.

The plot region is scaled from null to 100 percent, which represents the total species composition at each site. The area of the total plot region that is occupied by coloured boxes represents the percentage of non-overlapping species composition between the site pair (i.e. the 'remainder' in terminology explained earlier). The user can specify whether identical species overlap, the remainder or both should be shown. The *Renkonen* similarity and *Tsim* are included in each plot (in purple) for reference. An example of an AWH-plot for two sites dominated by *Acropora* is shown below (Figure 6.8).

The AWH-plot is a good way to visualize what species pairs are influencing the calculation of *Tsim* the most. The higher the *Gower similarity* (i.e. the more intense the colour of the box) the more likely it is that the species-pair will be selected for matching. The size of the box shows how much influence the species pairing (should it be selected) has on the overall *Tsim* calculation.

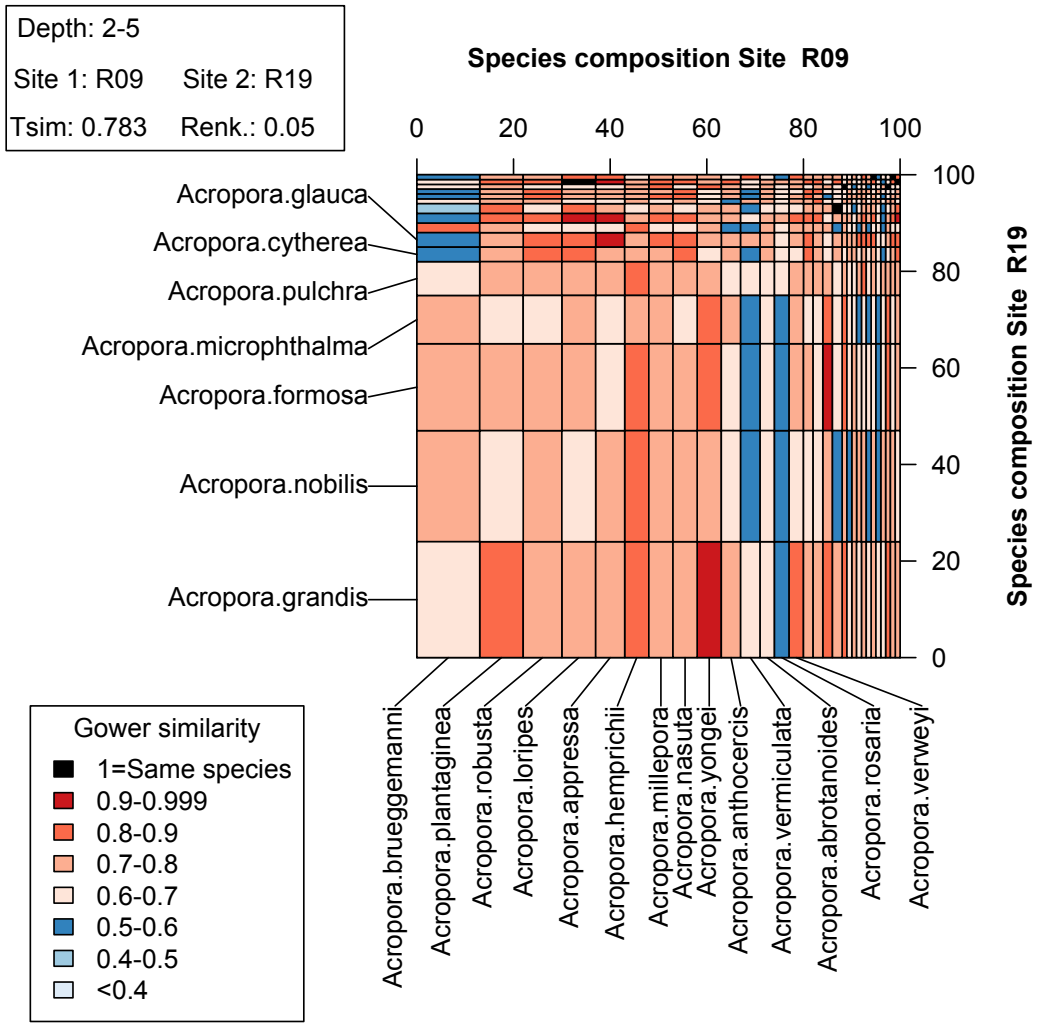


Figure 6.8 Example of Abundance Weighted Heat plot or AWH-plot. Note that species labels for species with abundance of two percent or less are not shown (16 *Acropora* sp. At R09 and 9 *Acropora* species at site R19. The R script for the E-plot function is available in Digital Supplement 1.3.

Please note how all three graph-types are related. Each site pair comparison made for a particular depth-zone is represented by one point in the scatter plot for that depth zone (Figure 6.2 to Figure 6.5). The sites highlighted in each scatter plot are then presented as an e-plot for each depth zone to show the influence of emergent groups on the Renkonen and *Tsim* scores. Finally, some of the site pairs highlighted in each scatter plot are shown as an AWH plot to highlight specific species-matches that may be influencing the overall trait similarity between the sites. All three visualization tools are available as **R** functions in Digital Supplement 1.3.

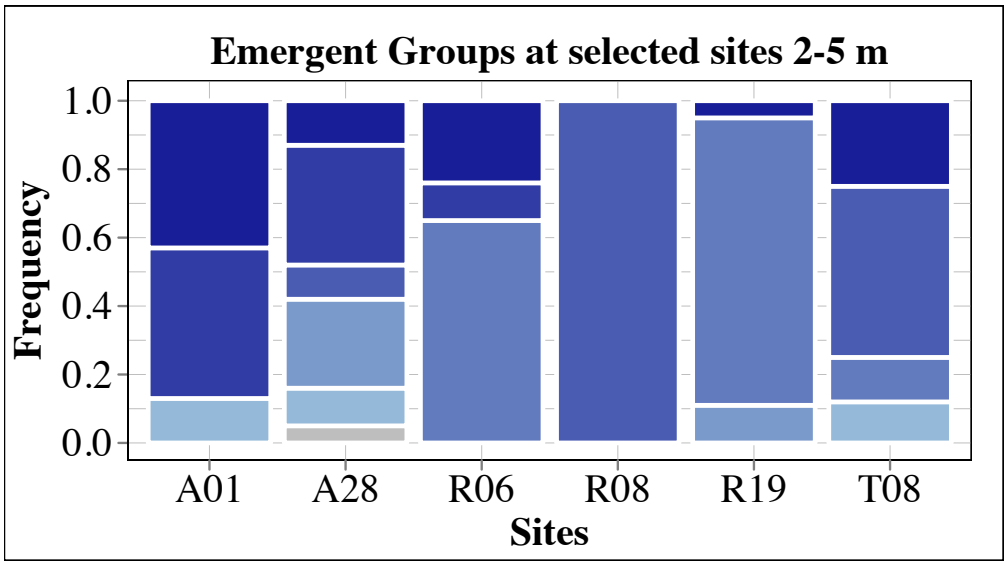
6.8. Results: Distribution of reefs in SW Madagascar in mechano-functional space

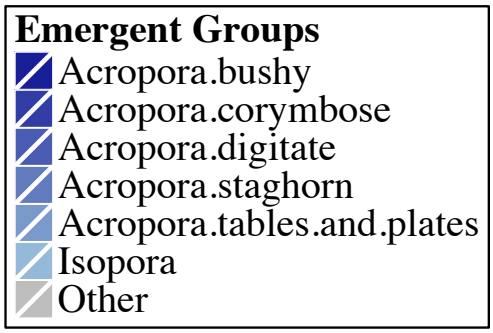
6.8.1. 2-5m depth zone

The species accumulation curves indicated that for the 34 sites with data available at two to five metres depth, 21 sites had sufficient data (93 points) to be included in further analysis resulting in 210 site pairs. These sites were located in all three study regions (Andava, Ranobe, Tulear).

Regions of the mf-space for this depth zone (see Figure 6.2) are now described. For simplicity regions of mf-space are referenced using their respective x (*Renkonen*) and y (*Tsim*) coordinates. The majority of site pairs occupied mf space *Renkonen* 0-0.2, *Tsim* 0.5-0.6. Site pairs in this region had low levels of species overlap and medium levels of trait similarity (*Gsim* ~0.6). These site pairs were neither functionally similar nor distinctly dissimilar in terms of the 26 traits considered.

The upper left hand section of the mf space represents the site pairs with the greatest functional similarity (*Tsim* of 0.7 - 1) across the spectrum of mechanical similarity (*Renk.* of 0 - 1). Site pairs in this plot region were dominated by *Acropora* species (see for example Figure 6.9). Given the high trait similarities between species in the *Acropora* species complex and the dominance of *Acropora* of shallow reef zones it is not surprising that they are responsible for the highest *Tsim* scores between site pairs. However, as the AWH-plots of site pairs in this region show, all *Acropora* are certainly not functionally equivalent and the *Gsim* between them can be quite variable (see for example *Acropora cuneata* in Figure 6.10).





	site.x	site.y	Renk.	Tsim
1	R06	R19	0.65	0.928
2	A01	A28	0.50	0.894
3	R06	T08	0.28	0.819
4	A28	R08	0.10	0.787
5	R08	R19	0.00	0.762

Figure 6.9 E-plot showing site pairs typical at two to five metres depth with high functional similarity (*Tsim* greater than 0.7) across the spectrum of mechanical similarity (*Renkonen* 0-1). *Acroporidae* are shown in blue and *s*pecies that do not belong to emergent groups are shown in the group 'other' in grey. The five site pairs shown here are also shown in Figure 6.2. The site pair A28-R08 is shown as a AWH plot in Figure 6.10. Note *Acropora*'s dominance at all six sites.

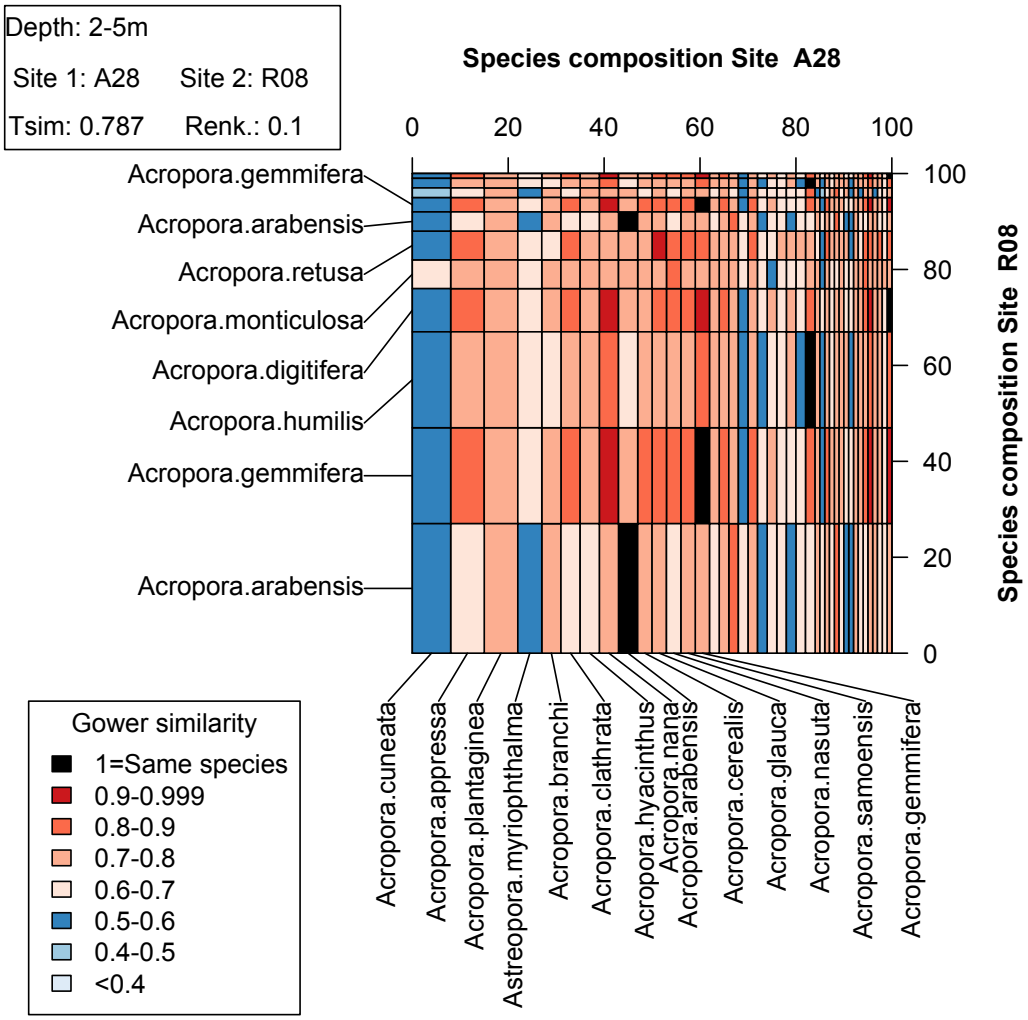


Figure 6.10 Abundance weighted heat plot for site A28 and R08 at two to five metres depth. Note the relatively high variability in *Gower similarity* between *Acropora* species showing that all *Acropora* are certainly not functionally equivalent. Species with two percent abundance or less are not shown (27 *Acropora* species at A28 and 3 species of *Acropora* at R08). Site pair A26-R08 is also shown in Figure 6.2 and Figure 6.9.

The lower left hand corner of the mf-space (*Renk.* 0-0.1, *Tsim* 0-0.4) contained site pairs with low mechanical and functional similarity; these sites can be considered truly ecologically dissimilar. An example of a site pair typical for this region of the mf-space is shown below (A28-T10; Figure 6.11). Note that site A28, which is dominated by *Acropora,* has similar *Renkonen* scores both when matched up with a functionally similar *Acropora* community at site R08 (Figure 6.10) and a functionally dissimilar *Cycloseris* dominated community (Figure 6.11). *Tsim* however makes a clear distinction between the two identifying the *Acropora*-

Acropora sites as functionally similar (*Tsim* of 0.787) and the *Acropora-Cycloseris* sites as functionally dissimilar (*Tsim* of 0.441).

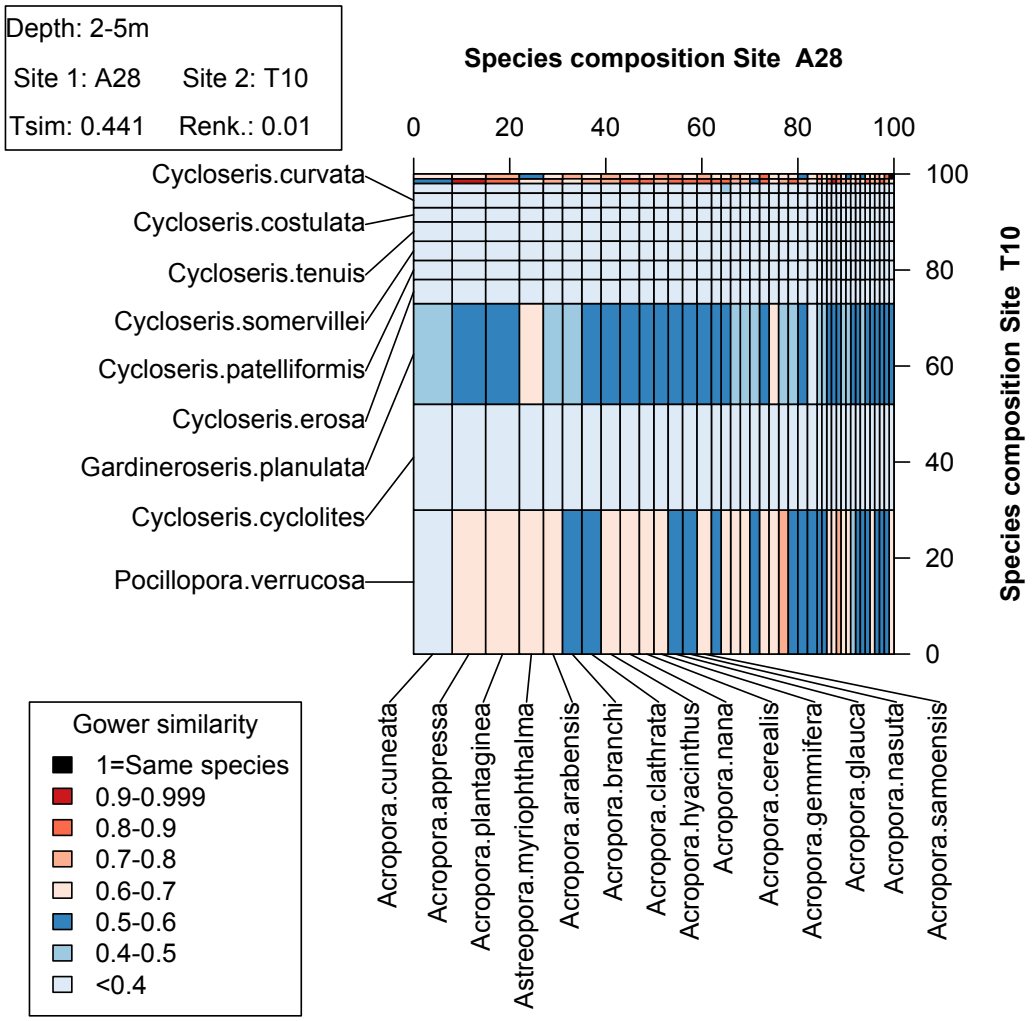


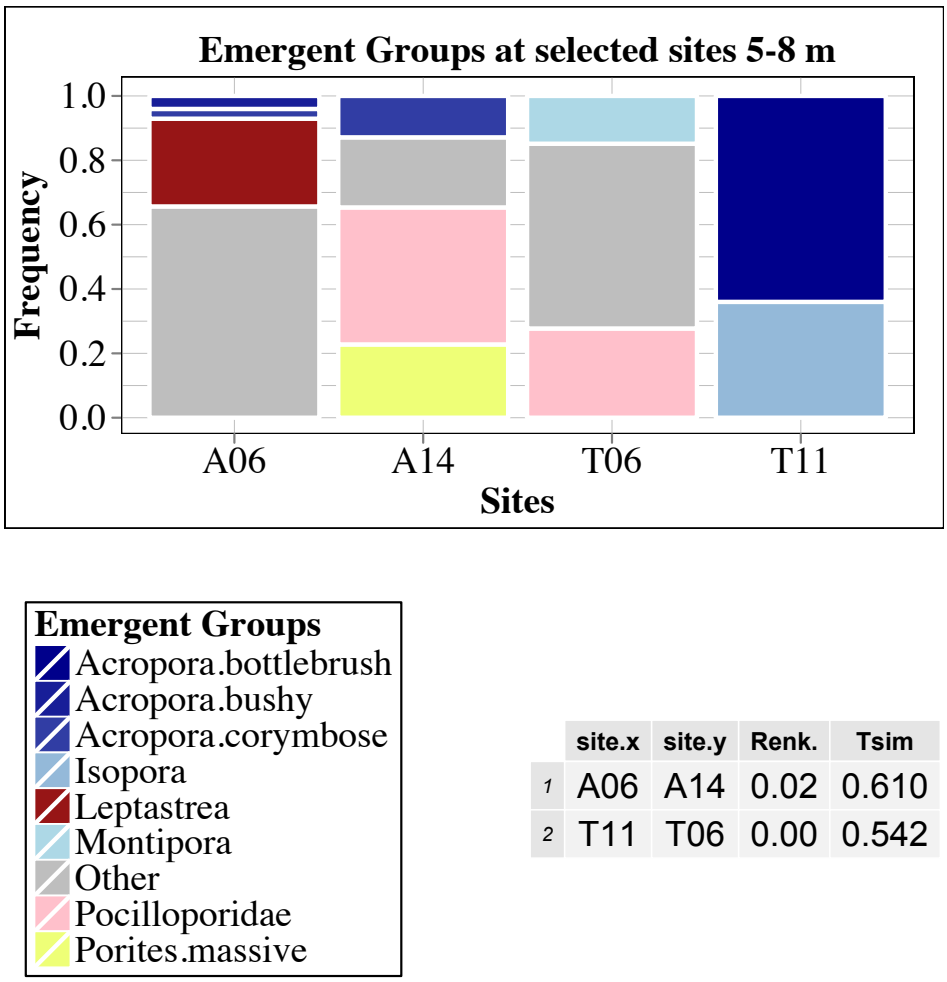
Figure 6.11 Abundance weighted heat plot for site A28 and T10 at two to five metres depth. Note that the *Renkonen* similarity and *Tsim* between the two sites is low and also that the *Gower similarity* between species pairs is low. These two sites are both mechanically and functionally dissimilar. Species with two percent abundance or less are not show: A28 27 *Acropora* species and T10 two *Acropora* species, and *Cycloseris vaughani*.

6.8.2. 5-8m depth zone

At five to eight metres depth, 45 sites had data available and 21 of these had data for 102 points or more, which is what the SACs indicated as a reasonable level at which to compare the sites. This resulted in 210 reef pairs. Coral coverage at this depth was

greater than at the two to five meter depth zone as competition from algae and heat stress was generally lower. Sites included 13 sites from Andava, two sites from inside the north section of the bay of Ranobe (edges of large patch reefs), and six reefs in Tulear.

Two examples of interesting site pairs are now discussed. They are first shown in the e-plot below and then in the two following AWH plots.



	site.x	site.y	Renk.	Tsim
1	A06	A14	0.02	0.610
2	T11	T06	0.00	0.542

Figure 6.12 The emergent group composition for four site pairs at the five to eight metre depth range. The *Tsim* and *Renkonen* similarity for each site pair is shown on the inset table. Emergent groups in the family *Acroporidae* are shown in blue and *Poritidae* in yellow. Additional emergent groups are shown in red. Species that do not belong to emergent groups are shown in the group 'other' in grey. The two site pairs shown here are also shown in Figure 6.3 and as AWH plots in Figure 6.13 and Figure 6.14.

The site pair distribution in the mf-space was similar to that for the two to five metre depth range, although it should be noted that *Tsim* scores were on average slightly higher. As with the two to five metre depth site pairs *Tsim* scores above 0.7 contained sites mainly dominated by *Acropora.* While site pairs with *Tsim* score less than 0.5 tended to compare *Acropora* dominated communities with functionally very different communities. One example of such a site pair is shown below (Figure 6.13).

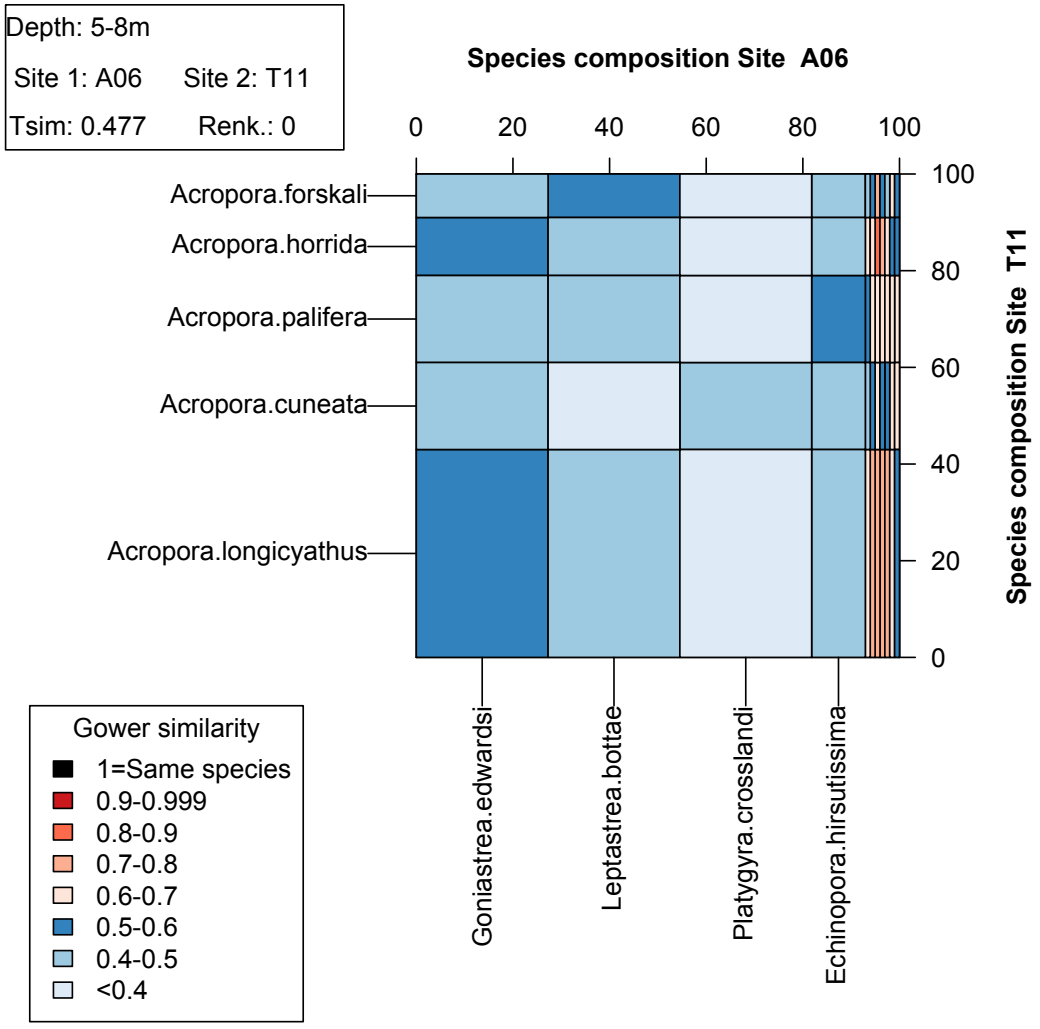


Figure 6.13 Abundance weighted heat plot for site A06 and T11 at five to eight metres depth. Note the *Renkonen* similarity and *Tsim* between the two sites is low and also that the *Gower* similarity between species pairs is low. These two sites are both mechanically and functionally dissimilar. Species with two percent abundance or less are not shown (seven *Acropora* species at A06). Site pair A06-T11 is also shown in Figure 6.3 and Figure 6.12.

Now that the extremes of the fm-space for this depth zone have been described, the focus can be turned towards identifying site pairs that are mechanically different but functionally similar and are not dominated by *Acropora.*

Sites A14 and T06 were both spur and groove systems with steep bulky spurs and short wide grooves. Interestingly these sites were functionally highly similar (*Tsim* 0.711) despite having few species in common (*Renk*. = 0.069). Site A14 is located outside the barrier island of Nosy Hao in the north while site T06 is located outside the Tulear barrier reef. The AWH-plot for the site pair is shown below (Figure 6.14)

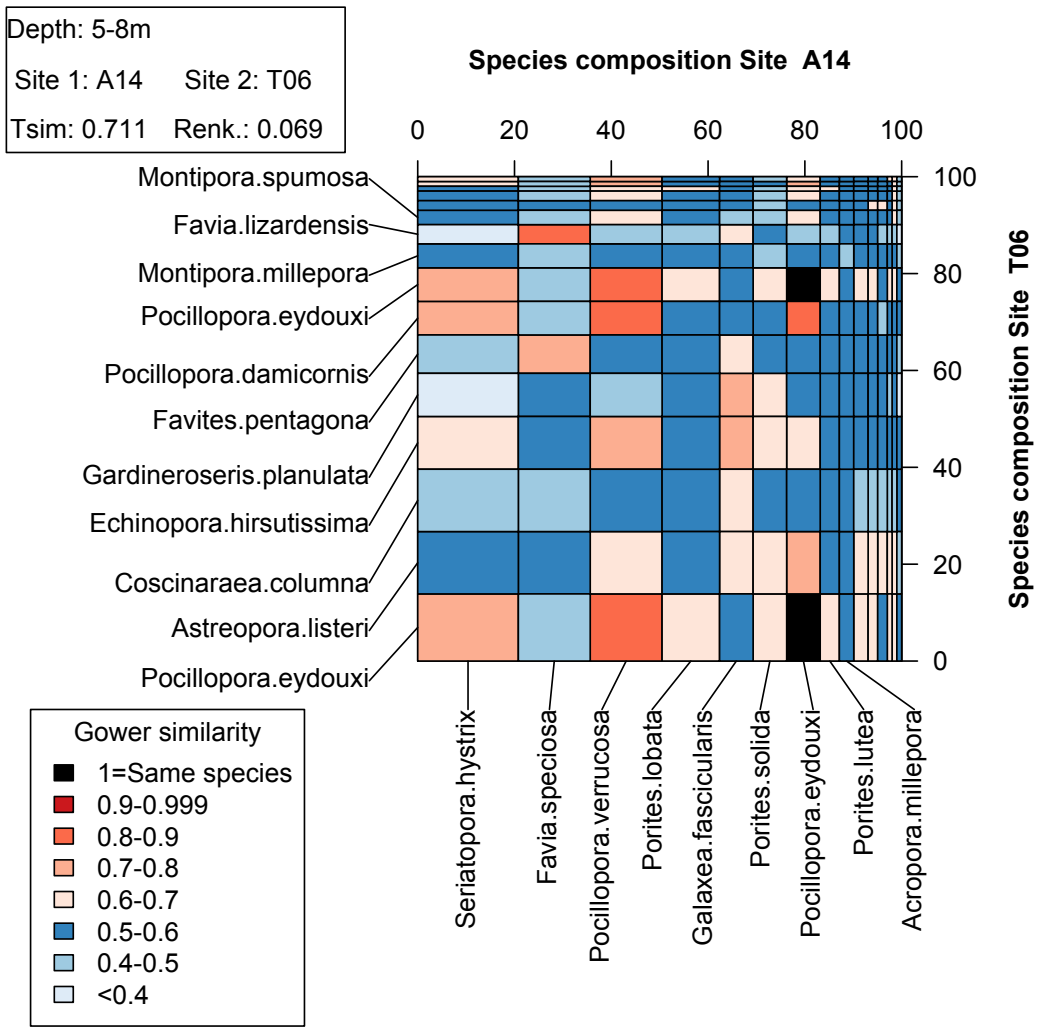


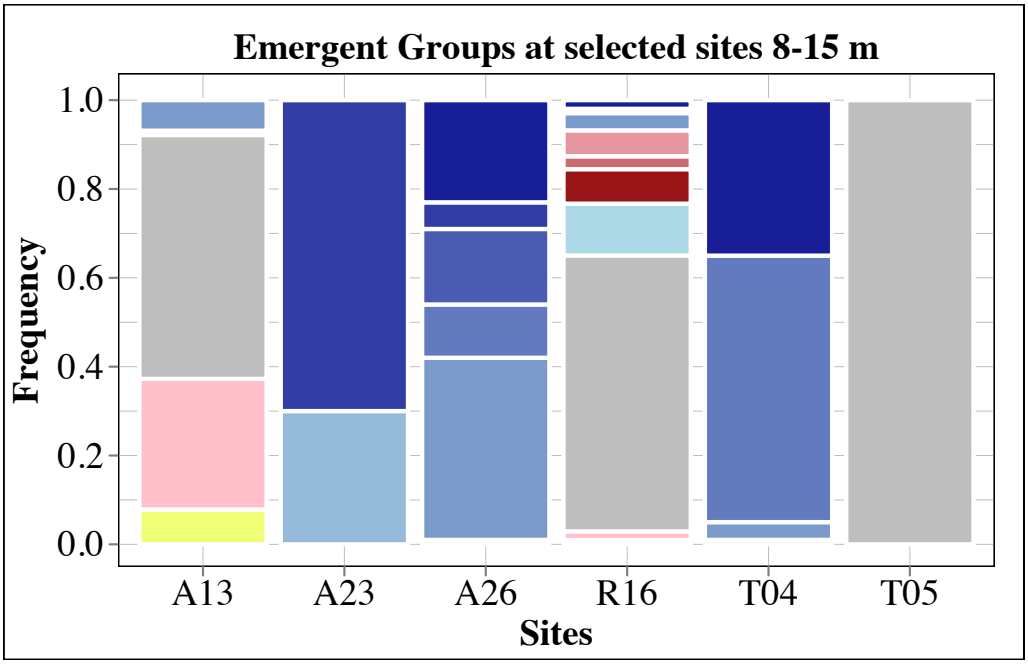
Figure 6.14 Abundance weighted heat plot for site T06 and A14 at five to eight metres depth. Note the high functional similarity (*Tsim* = 0.711) despite the low mechanical similarity (*Renkonen* = 0.069). For clarity the labels for species with less than two percent abundance or less are not shown (five *Acropora* species at A14 and five *Montipora* species at T06). Site pair T06-A14 is also shown in Figure 6.3 and Figure 6.12.

The AWH-plot suggests the following matches are largely influencing the overall value of *Tsim*: *Pocillopora eydouxi-Pocillopora verrucosa* (14 percent overlap, *Gsim* = 0.884), *Favia speciosa-Favia lizardensis* (four percent overlap, *Gsim* = 0.872), *Pocillopora damicornis-Seriatopora hysterix* (seven percent overlap, *Gsim* = 0.780), *Favia speciosa-Favites pentagona* (eight percent overlap, *Gsim* = 0.738), *Galaxea fasicularis-Gardinoseris planulata* (seven percent overlap, *Gsim* = 0.737).

6.8.3. 8-15m depth zone

Data are available for 44 sites for the eight to 15 metre depth zone, and 34 sites had sufficient data to be compared at a sampling effort of 96 points, which was that indicated to be the best compromise between including sites and levelling off of the SACs. The 34 sites included resulted in 561 site pairs.

Due to the very large number of site pairs available at this depth zone not all types of functionally similar but mechanically different sites can be described here. However, a number of site pairs that are interesting and representative are discussed. The emergent group compositions for the site pairs are shown in Figure 6.15



Emergent Groups

- Acropora.bushy
- Acropora.corymbose
- Acropora.digitate
- Acropora.staghorn
- Acropora.tables.and.plates
- Bubble.Coral
- Fleshy.Domes
- Isopora
- Leptastrea
- Montipora
- Other
- Pocilloporidae
- Porites.massive

	site.x	site.y	Renk.	Tsim
1	A23	A26	0.060	0.793
2	A13	T05	0.098	0.718
3	R16	T05	0.010	0.713
4	T05	T04	0.000	0.491

Figure 6.15 The emergent group composition for five example site pairs for the eight to 15 metre depth range. The *Tsim* and *Renkonen* similarity for each site pair is shown on the inset table. Emergent groups in the family *Acroporidae* are shown in blue, *Poritidae* in yellow. Additional emergent groups are shown in red. Species that do not belong to emergent groups are shown in the groups 'other' in grey. The four site pairs are also shown in Figure 6.4 and as AWH plots in Figure 6.16 to Figure 6.18 and Figure 6.20.

Like with the previous depth zones the site pairs with the highest *Tsim* scores were dominated by *Acropora*. Sites with similar *Acropora* species clusters (i.e. *Acropora*

branching) tended to have higher *Tsim* scores than those that had different *Acropora* species clusters. Also sites with species in the *Isopora* emergent group (i.e. *Acropora cuneata* and *Acropora palifera*) tended to downweight the *Tsim* scores between *Acropora* dominated communities.

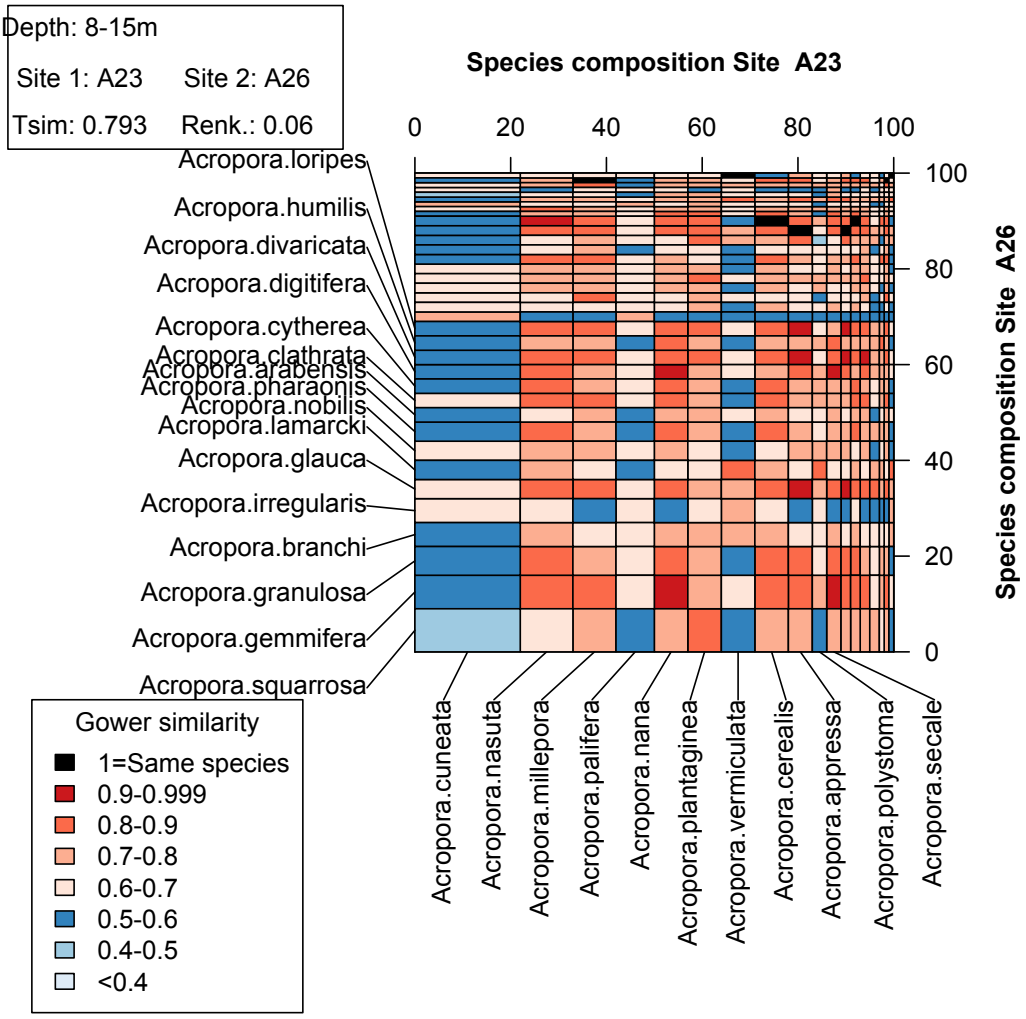


Figure 6.16 AWH plot for site pair A23-A26 at eight to 15 metres depth. Labels for species with less than two percent abundance are not show for clarity this includes: seven Acropora species at A23 and 20 *Acropora* species at A26. The site pair A23-A26 is also shown in Figure 6.4 and Figure 6.15.

For the 8-15 m depth zone it was common to find site pairs that were dominated by species not belonging to emergent groups (see for example site pairs A13-T05, R16-T05, and T05-T04 in Figure 6.15) These site pairs where particularly interesting because the high level of trait similarity between sites was not immediately obvious.

Site A13 and T05 are both spur and grove systems exposed to similar environmental conditions (they are located outside the barrier reef and experience strong currents and low levels of sedimentation due to flushing). Both are dominated by species not belonging to emergent groups yet they have a high level of functional overlap (*Tsim* = 0.718) despite low species overlap (*Renkonen* = 0.098). This is due to the matching (Figure 6.17 of the following dominant species *Favia lizardensis-Favia rotumana* (*Gsim* = 0.8402), *Galaxea fasicularis-Montastrea colemani* (*Gsim* = 0.746), *Pocillopora verrucosa-Echinopora hirsutissima* (*Gsim* = 0.702). Note that all of the dominant species at both sites (with the exception of *Pocillopora damicornis*) have relatively high trait similarity, most likely because they occupy similar environmental niches.

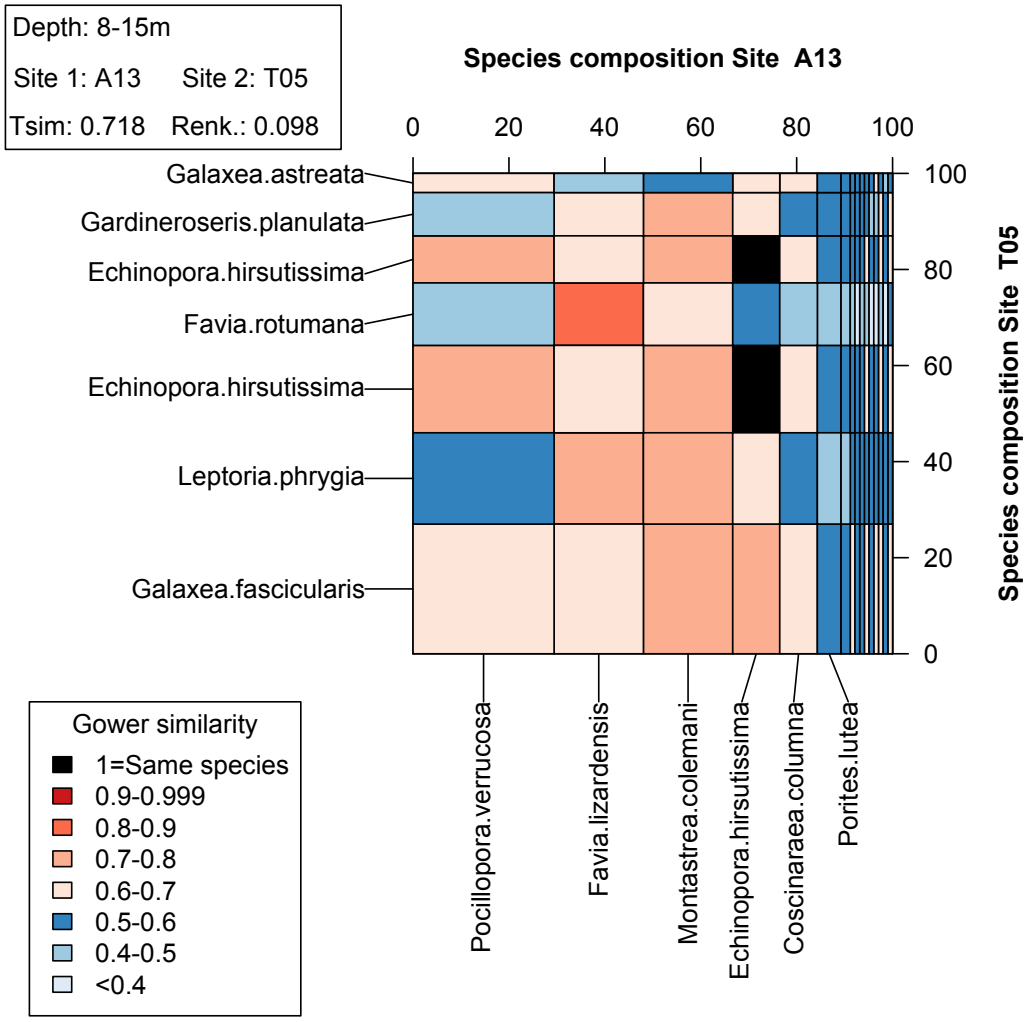


Figure 6.17 AWH plot for site pair A13-T05 at eight to 15 metres depth. Labels for species with two percent abundance or less are not shown for clarity. This included nine *Acropora* species and *Porites solida* at A13. Site pair A13-T05 are also shown in Figure 6.4 and Figure 6.15.

Site R16 is a unique formation of coral pillars located in the south pass of the Ranobe barrier reefs. Due to its position in the middle of the pass it experienced high levels of flushing and is also difficult to fish using traditional Vezo pirogues. Site T05 is a spur and groove system located outside the northern section of the Tulear barrier reef.

Despite having very low species overlap (*Renkonen* = 0.01) the two sites are functionally quite similar (*Tsim* = 0.713). This is due to high *Gsim* scores between many species pairs (see Figure 6.18). For example: *Favia speciosa-Favia rotumana*

(10.7 percent overlap, *Gsim* = 0.890), *Diploastrea heliopora-Echinopora hirsutissima* (13.6 percent overlap, *Gsim* = 0.734), *Goniastrea retiformis –Leptoria Phrygia* (eight percent overlap, *Gsim* = 0.736), *Montastrea curta - Echinopora hirsutissima* (six percent overlap, *Gsim* = 0.748), *Montastrea colemani-Galaxea fasicularis* (six percent overlap, *Gsim* = 0.746), and *Physogyra lichtensteini-Galaxea fasicularis* (seven percent overlap, *Gsim* = 0.727).

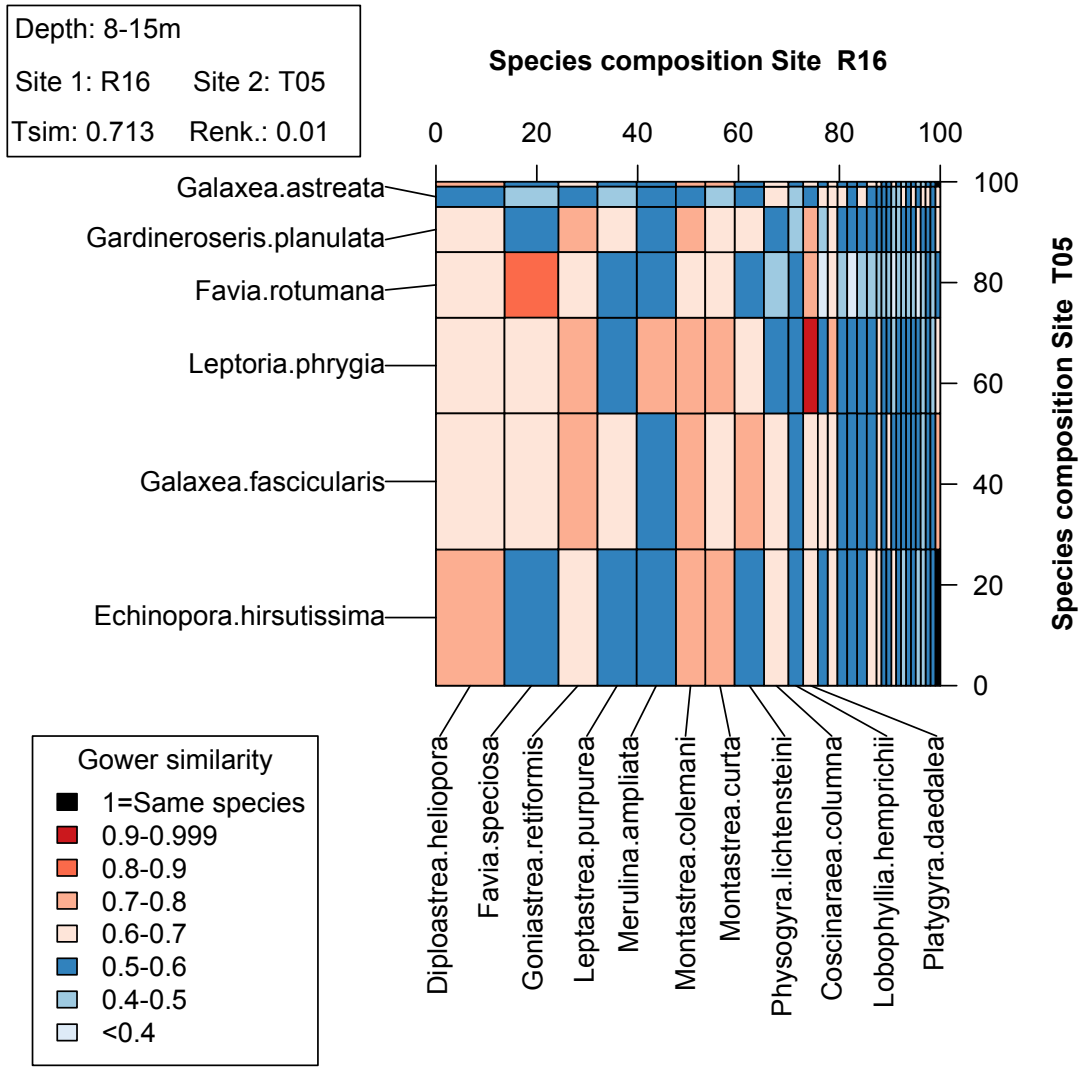


Figure 6.18 AWH plot for site pair R16-T05 at eight to 15 metres depth. Labels for species with two percent abundance or less are not shown for clarity. At R16 this included six *Acropora* species, nine *Montipora* species, *Astreopora myriophthalma*, *Pocillopora eydouxi*, *Echinopora hirsutissima*, and Porites lutea. This also includes the one percent overlap between the sites for *Echinopora hirsutissima*. Note that the *Echinopora hirsutissima* in the reminder of T05 is still labelled, as it comprised aroun 27 percent of the species composition at T05. Site pair R16-T05 are also shown in Figure 6.4 and Figure 6.15.

The site pair T05 and T04 give an example of how two sites that are near one another geographically can experience very different environmental regimes, which results in very different mechanical and functional communities. Site T04 is located in a 20 metre deep hole in the Tulear barrier reef while T05 is located less than 2 km to the Southwest, but importantly, outside the barrier.

Figure 6.19 Satellite image showing the location of site T04 relative to T05. T04 is located in a 20 metre deep 'hole' in the northern part of the Tulear barrier while T05 is located less than two kilometres southwest of T05 but outside the barrier.

These two sites have no overlap in species (*Renkonen* = 0). However, as has been demonstrated in previous examples, low or no species overlap does not necessarily imply that the sites are not functionally similar. So using *Tsim* here one can verify that the two sites are in fact both mechanically and functionally different (notice the low *Gower similarities* between most species pairs in Figure 6.20).

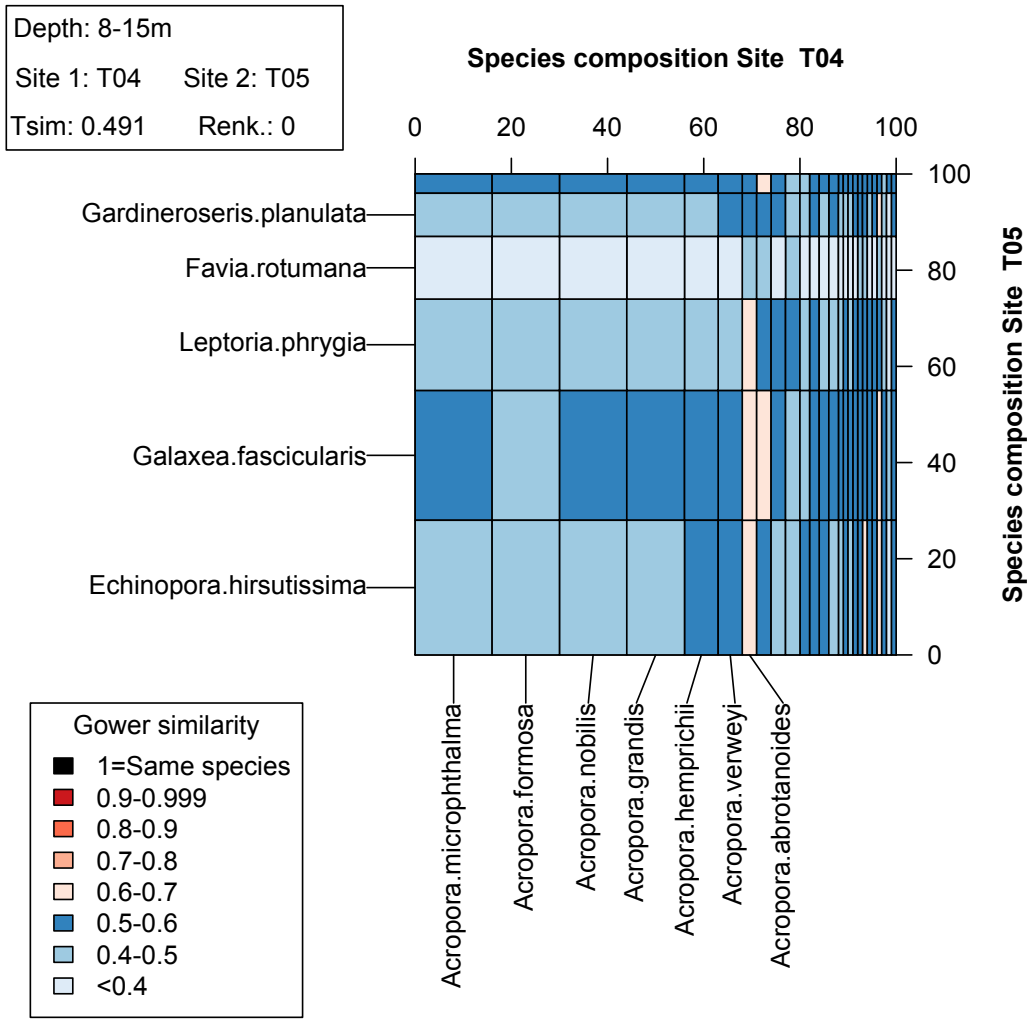
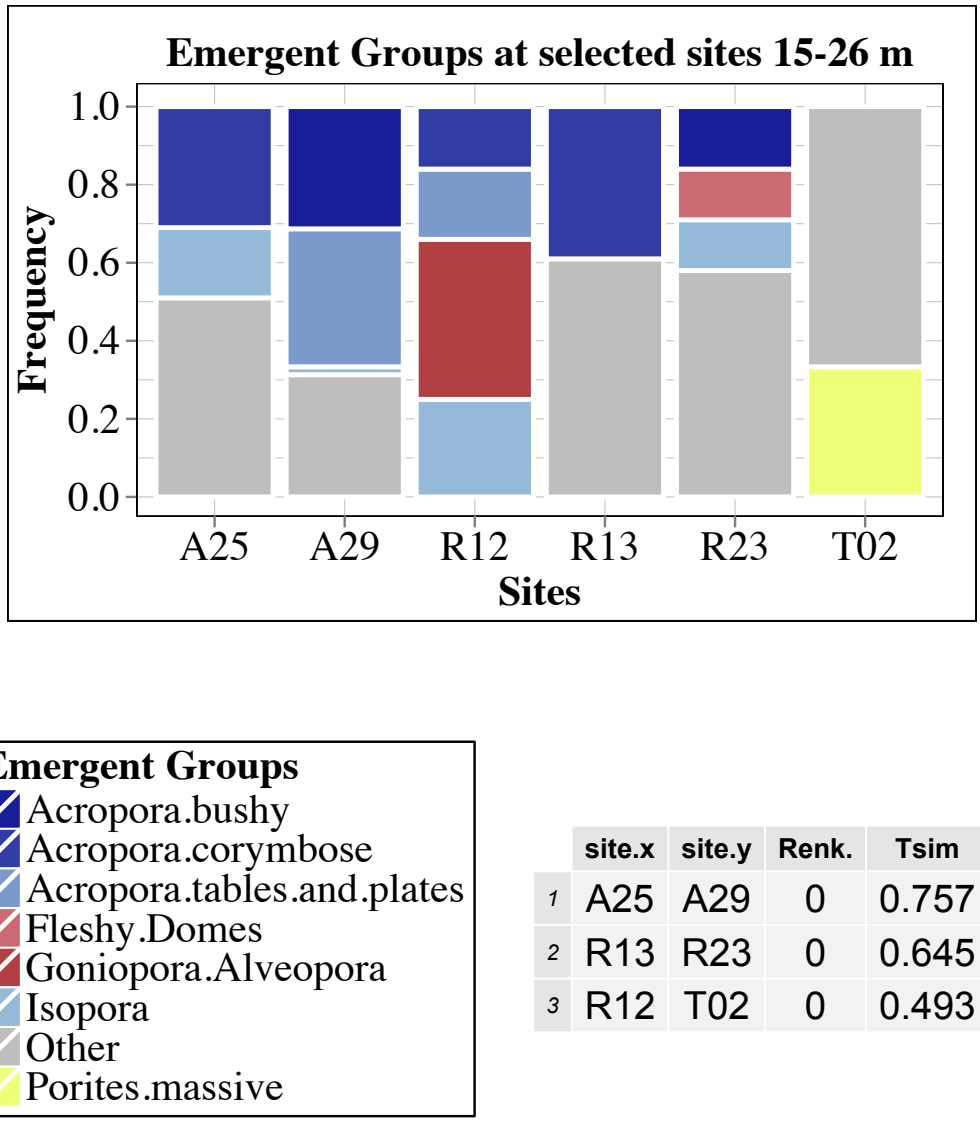


Figure 6.20 AWH plot for site pair T05-T04 at eight to 15 metres depth. These two sites are both functionally and mechanically dissimilar as can be seen by the lack of overlapping species and the low *Gsim* scores between species pairs. Site pair T04-T05 are also shown in Figure 6.4, Figure 6.15 and Figure 6.19.

6.8.4. 15-26m depth zone

Data was available for 22 sites at 15-26m depth and 17 sites had data available at 54 points, which was determined from examining the SACs to be a reasonable sampling effort at which to compare the data. The 17 sites resulted in 136 site pairs.

Acropora was not as dominant for this depth zone and therefore the site pairs with the highest *Tsim* scores relative to *Renkonen* scores were not entirely dominated by *Acropora* (as can be seen in Figure 6.21).



	site.x	site.y	Renk.	Tsim
1	A25	A29	0	0.757
2	R13	R23	0	0.645
3	R12	T02	0	0.493

Figure 6.21 Emergent group composition for select site pairs at 15 to 26 metres depth. The *Tsim* and *Renkonen* similarity for each site pair is shown on the inset table. Emergent groups in the family *Acroporidae* are shown in blue, *Poritidae* in yellow. Additional emergent groups are shown in red. Species that do not belong to emergent groups are shown in the groups 'other' in grey. The three site pairs are also shown in Figure 6.5 and as AWH plots in Figure 6.22 to Figure 6.24.

Site pairs that were mechanically similar but functionally different tended to match *Acropora* with *Astreopora, Echinopora* and other encrusting species. The site pair A25-A29 provides an example of such a match (see Figure 6.22). Both sites are exposed to the Southwest current and are difficult to fish: A25 because it is protected as a marine reserve and A29 because of the difficulty of finding the site.

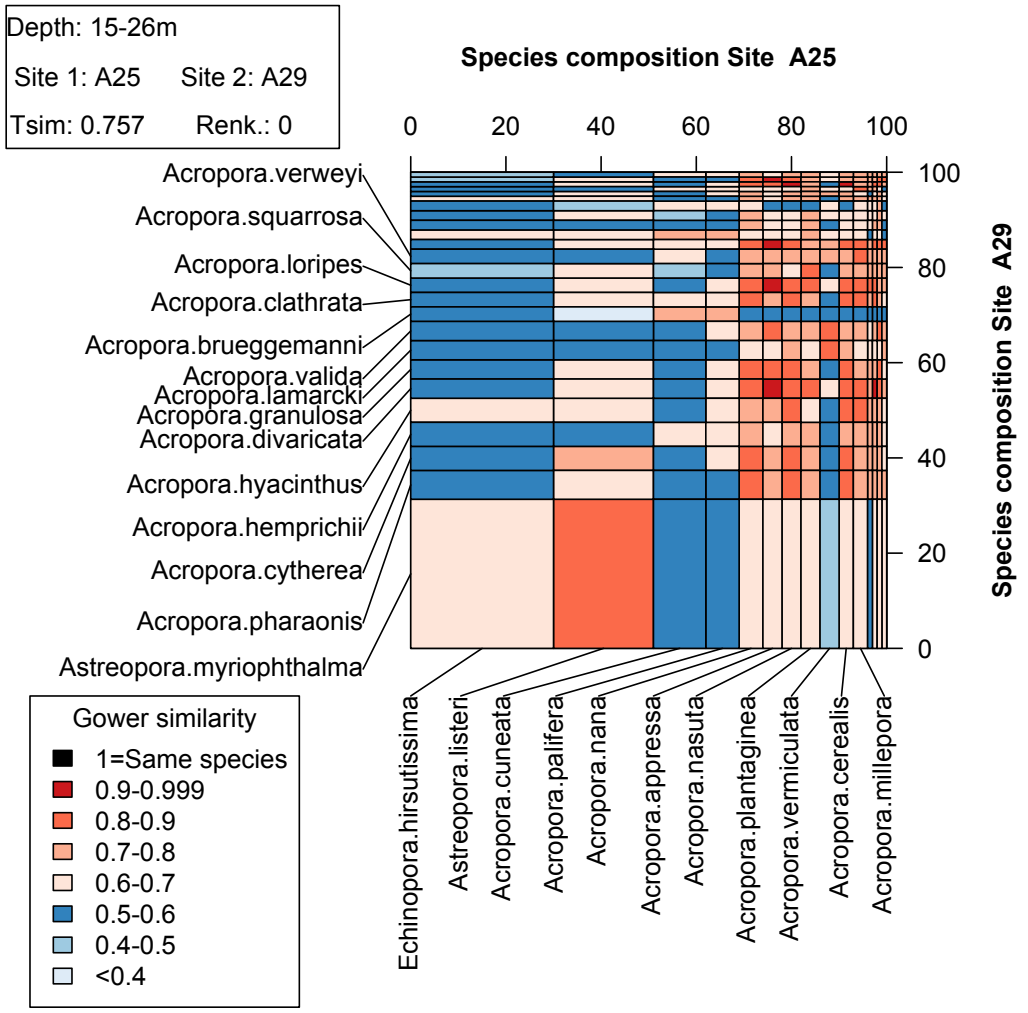


Figure 6.22 AWH plot for site pair A25-A29 at a depth of 15 to 26 metres. Labels for species with two percent abundance or less are not shown. For site A25 this included four *Acropora* species and for site A29 it included 11 *Acropora* species. Site pair A25-A29 is also shown in Figure 6.5 and Figure 6.21.

Site R13 and R23 are gently sloping spur and groove systems located outside the Ranobe barrier reef. *Astreopora myriophthalma* makes up 61 percent of the species composition at site R13 and this matches up with *Favites pentagona* (13 percent overlap, *Gsim* = 0.721), *Echinopora hirsutissima* (13 percent overlap, *Gsim* = 0.686) and *Echinopora forskaliana* (13 percent overlap, *Gsim* = 0.789). The remaining *Echinopora forskaliana* matches up with *Acropora* species. In addition match-ups between *Acropora* at both increase the total *Tsim* score (see Figure 6.23).

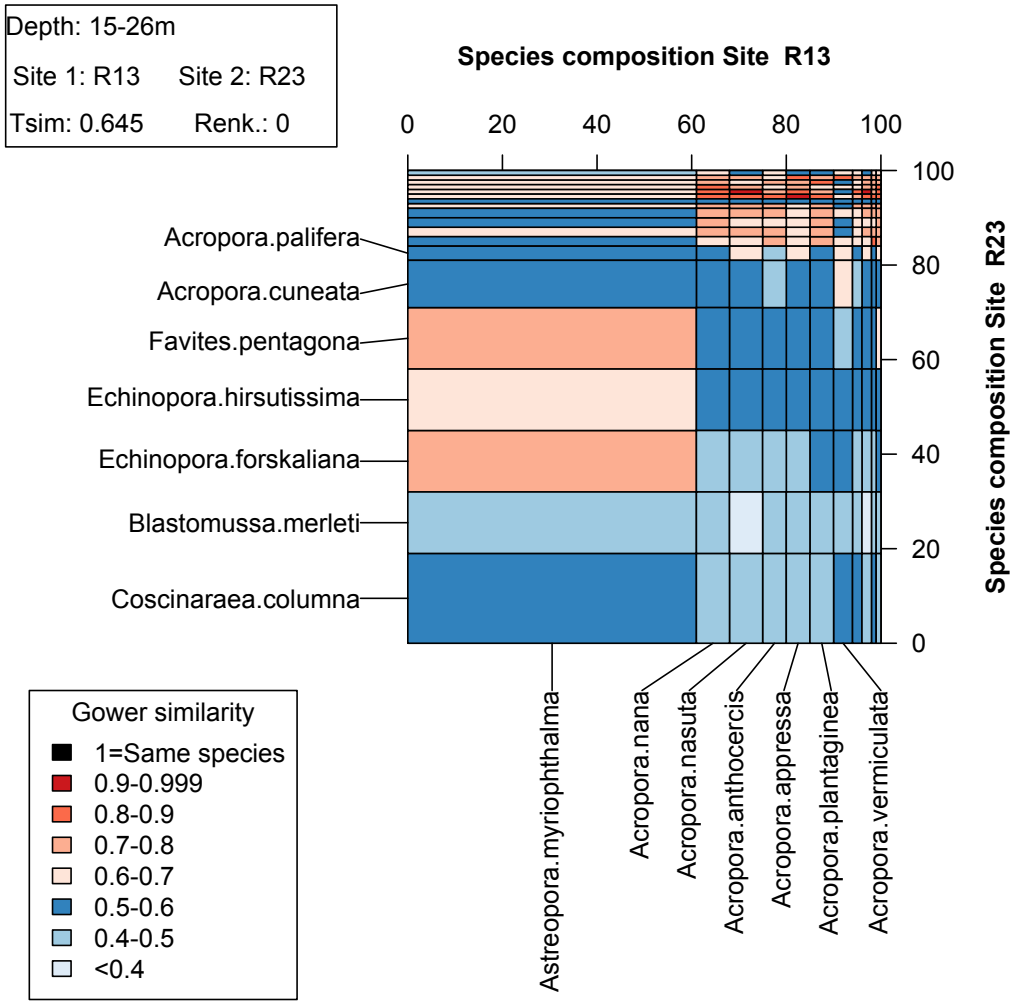


Figure 6.23 AWH plot for site pair R13-R23 at a depth of 15 to 26 metres. Labels for species with two percent abundance or less are not shown for clarity. For R13 this included four *Acropora* species, while for R23 this included 12 *Acropora* species. Site pair R13-R23 is also shown in Figure 6.5 and Figure 6.21.

Finally, site R12 and T02 provide an example of site pairs at this depth that are both mechanically and functionally dissimilar (see Figure 6.24) despite both of these sites being spur and groove systems. *Alveopora* and *Acropora* species dominated site R12 while T02 was dominated by massive *Porites* species, *Oulophyllia crispa* and *Astreopora myriopthalma* all of which have low levels of trait combination overlap.

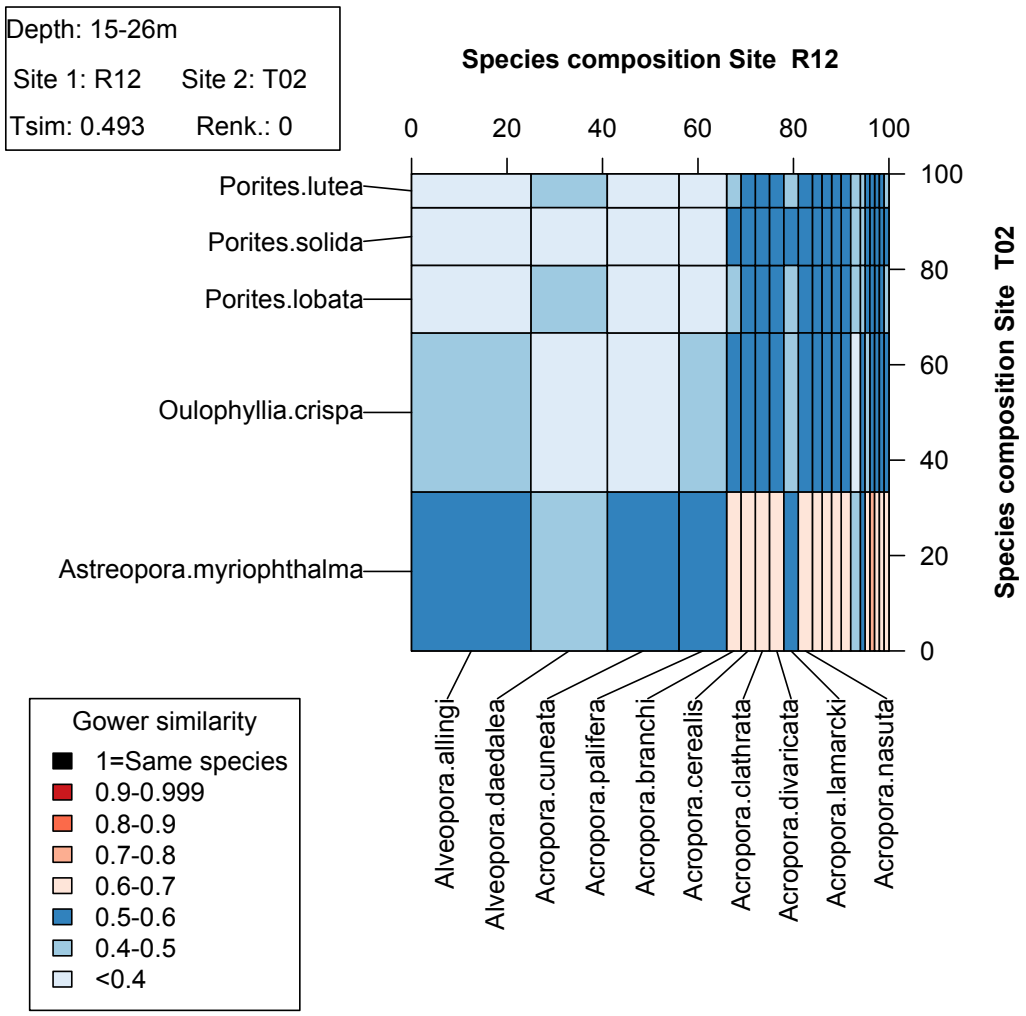


Figure 6.24 AWH plot of site pair R12-T02 at a depth of 15 to 26 metres. Labels for species with two percent abundance or less are not shown for clarity. This included 11 *Acropora* species at R12. Site pair R12-T02 is also shown in Figure 6.5 and Figure 6.21

6.9. Discussion

In this chapter I presented a new similarity measure, *Tsim*, which takes a fundamentally novel approach to estimating site similarity. It does so by going beyond the simplistic approach of species similarity metrics, which consider species to be either entirely similar or entirely dissimilar and instead respects the point that species exist on a continuum of similarity and dissimilarity with respect to their life-history traits.

A package of functions programmed in **R** were presented consisting of:

- **Tsim ()** which calculates the *Tsim* and *Renkonen* similarity between sites,
- **tr.plot()** which plots *Tsim* against the *Renkonen* thereby showing site pairs in mechno-functional space,
- **e.plot()** which plots the emergent group compositions for site–pairs of a select region of the mechano-funcional space and
- **awh.plot()** which plots abundance weighted heat maps for site pairs, in effect visualizing the *Tsim* calculation.

It is hoped that this package of functions, in combination with the coral trait database, will allow researchers to easily supplement their species-based similarity metrics with a trait-based similarity metric. In doing so they will ensure that they are not missing sites that are functionally similar despite being mechanically different.

Three key concepts associated with *Tsim* are now discussed: the importance of trait combinations, functional redundancy, and response diversity. The practical use of *Tsim* in surveying Marine Protected Areas (MPAs) and potential extensions and future work are then briefly discussed.

6.9.1. Traits vs. Trait Combinations

Due to the computational simplicity it is tempting to translate species composition directly into trait composition by multiplying a site-species matrix by a species-trait matrix thereby producing a site-trait matrix. However, this is inappropriate because traits are ‘packaged’ within the species unit and cannot be considered as independent

entities. Traits pass through environmental filtering events (such as warming events) in particular combinations, while species pass through such filters individually (see Figure 6.25). Therefore it is critical that any similarity measure of trait composition takes the 'packaging' of traits into account; *Tsim* adheres to this criterion.

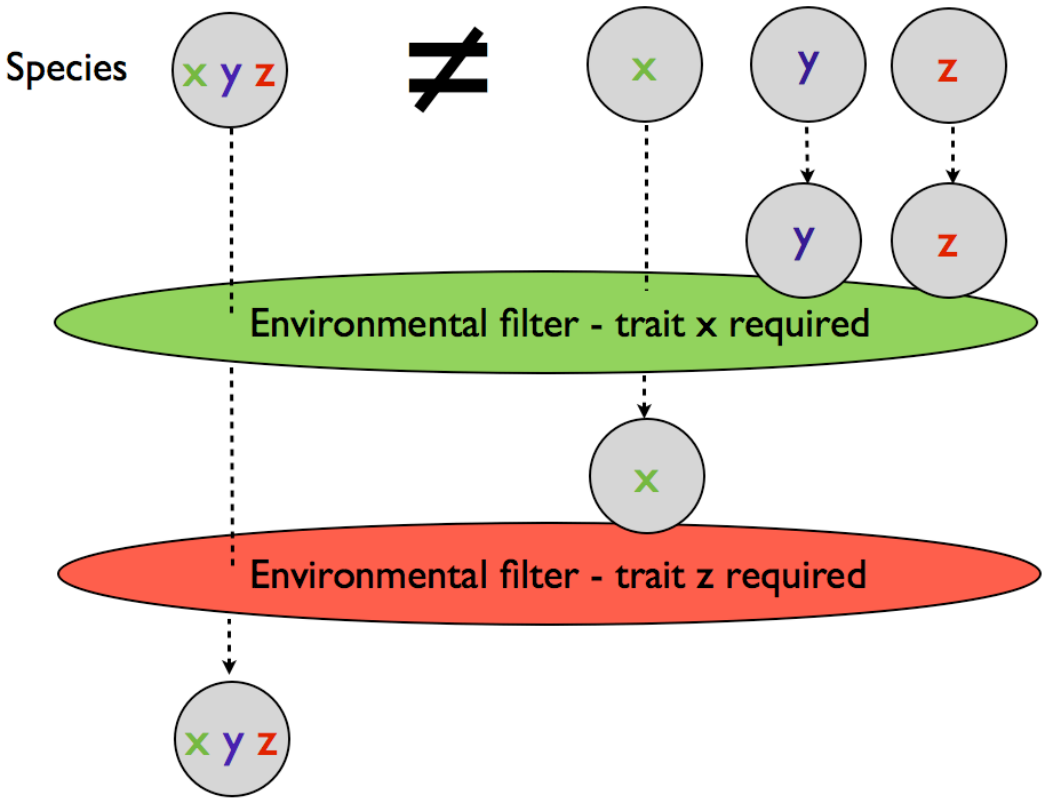


Figure 6.25 Diagram showing that traits (i.e. x, y, z) pass through environmental filtering events (warming events, storms etc.) 'packaged' within species (grey circles). Therefore possessing particular trait combination rather than individual traits determines the success of species persisting over time. *Tsim* respects this fact by not 'unpackaging' traits from the unit of the species.

6.9.2. Traits, functional redundancy, and response diversity

The term 'functional similarity' has been used quite loosely in this chapter to refer to the similarity between reefs in regards to the trait-combinations of their coral species composition for the 26 life-history traits that currently make up the coral trait database. The traits used in this study undoubtedly influence many reef processes and thereby the overall functionality of reefs (where functionality is considered simply as the continuation of existing processes and maintaining the reef in a

relatively stable state). So in this chapter when I suggest that reefs are 'functionally' similar I am referring to ecosystem 'functionality' in the broadest sense.

It is possible however to get much more specific. As discussed in Chapter Two, knowledge of coral traits and their relationship to reef processes and environmental stressors is rapidly growing. If one can link a particular set of traits to a particular reef function one can use *Tsim* as an estimate of the 'functional redundancy' between reefs for that function. Likewise if one can link a particular set of traits to either the resistance to, and/or recovery from, specific environmental stressors then one can use *Tsim* as an estimate of 'response diversity' to that particular stressor.

It is conceivable, then, that in determining how similar or dissimilar reefs are overall in terms of functional redundancy and response diversity, one would need to use a series of *Tsim* scores that refer to different and specific functions and stressors. *Tsim* can easily be calculated for any combination of the 26 traits in the trait database. Practically this involves simply filtering the species-trait matrix that is required by the **Tsim()** function. Traits can also be weighted if they are not all equally important to the ecological function or response in question.

6.9.3. Tsim in reef surveys and monitoring

One key step in both the initial surveying and continued monitoring of reefs (and MPAs are a good example) is to establish the levels of functional redundancy and response diversity for reefs within the area concerned. This is currently done via species-based surveys, using species-based similarity measures and diversity metrics and then loosely drawing the connection between particular species and functions and/or responses. The *Tsim* package allows for easy translation of hard-earned species abundance data into a concrete similarity measure of functional redundancy and response diversity which, in turn, can be used as the basis for a multivariate statistical analysis (as demonstrated in the following chapter). Ultimately this allows for both the direct analysis and visualization of functional redundancy and response diversity for reefs in an MPA.

6.9.4. Future work

The *Tsim* package and trait database serve as a foundation for moving trait-based ecology forward in reef ecology. What is needed now is continued study and compiling of coral traits into an online trait-database. Also, continued research is needed to more firmly establish existing links between traits and functions and potentially reveal new trait-function links.

7.
Trait vs. Renkonen based ordinations of reef sites

7.1. Introduction

In this chapter I examine if and how trait-based ordinations, more specifically Principal Coordinates Analyses (PCoA) and Non-metric Dimensional Scalings (NMDS), for Southwest Madagascar differ from species-based ordinations and whether these differences are more, or less, representative of the true ecological situation. In other words: is a trait-based similarity measure 'better' than a species-based similarity measure in terms of representing true site-similarity between reefs in terms of their coral communities?

7.2. Methods

An ordination can be thought of as a map of samples in two or more dimensions in which the placement of samples represents their similarity to one another. Ordinations can be carried out using either a similarity or dissimilarity matrix. Similarity coefficients commonly range either from null to one or null to 100 where null is no similarity (i.e. complete dissimilarity) and one or 100 is complete similarity (i.e. no dissimilarity). Dissimilarity coefficients also range from null to one or null to 100 but here null is no dissimilarity (i.e. complete similarity) and one or 100 is complete dissimilarity (i.e. no similarity).

Dissimilarity and similarity are complements such that one (or 100) minus similarity gives dissimilarity and vice versa. Within the R platform, dissimilarities are standardly used for computing ordinations such as PCoA and NMDS. Therefore, the Trait similarity measure (*Tsim*) and Renkonen similarity measure (*Rsim*) will be discussed in this chapter in terms of their complements: the Trait dissimilarity measure (hereafter *Tdis*) and the Renkonen dissimilarity measure (hereafter *Rdis*). (NB using the *Tdis* and *Rdis* rather than *Tsim* and *Rsim* has no impact on the positioning of the sites in space).

Several methods for creating ordinations include: Principal Component Analysis (PCA), Correspondence Analysis (CA), Detrended Correspondence Analysis (DECORANA), Principal Co-Ordinate Analysis (PCoA), Multi-Dimensional Scaling (MDS) and Non-metric Multidimensional Scaling (NMDS). As only PCoA and NMDS are flexible enough for use with any distance measure these two methods were selected for carrying out the ordinations.

Both PCoA and NMDS are common ordination methods (Legendre and Legendre, 1998). The computational details will therefore not be explained here, however, a general overview of both PCoA and NMDS are given in the next two sections along with the details of how the PCoA and NMDS were implemented for *Tdis* and *Rdis* for the four depth zones considered (2-5 m, 5-8 m, 8-15 m, and 15-26 m; NB PCoA and NMDS are purely descriptive methods and therefore it is not possible to determine the statistical significance of the structures they identify).

7.2.1. Principal coordinate analysis (PCoA)

PCoA is an eigen-vector method devoted to ordination of distance matrices and allows the user great flexibility in terms of the association measure used. However, if the dissimilarity measure is non-euclidean then the PCoA may react by producing several negative eigenvalues, therefore the Euclidean nature of both *Tdis* and *Rdis* were tested using the **is.euclid()** function in the ade4 package of R. Neither *Tdis* nor *Rdis* were Euclidean according to Gower's theorem (Gower and Legendre, 1986).

Two technical solutions have been suggested to deal with this issue: 1) adding a constant to the squared distances among sites (Lingoes correction; Lingoes, 1971) or 2) directly to the distances themselves (Cailliez correction; Cailliez, 1983). PCoAs were calculated for the *Tdis* matrix and *Rdis* matrix for each depth zone using both correction methods (implemented via the **cmdscale()** function in the stats package in R). For all depth zones the Lingoes and Cailliez corrections produced very similar results in terms of the amount of variation captured by the first two axes; the Caillez was just slightly better and therefore selected. The amount of variation that the first

two eigenvectors of the PCoA captured using the Caillez correction for *Tdis* and *Rdis* for the four depth zones is summarized in Table 7.1.

Table 7.1 Variability of the dissimilarity matrices at each depth represented by the first two eigenvectors of a PCoA when using the Caillez correction (higher numbers indicates that the ordination represents the data better).

Depth zone	**PCoA: variability captured by first 2 eigenvectors (*Tdis)***	**PCoA: variability captured by first 2 eigenvectors (*Rdis)***
2 - 5 m	0.4884	0.2814
5 - 8 m	0.4236	0.2867
8 - 15 m	0.3930	0.2746
15 - 26 m	0.3747	0.3782

For all but depth zone 15 to 26 metres *Tdis* produced better PCoA representations than *Rdis*. Even though *Tdis* represented more of the data variation than *Rdis* overall the amount of variability represented by the first two axes of the PCoA were rather low for both dissimilarity measures, therefore an NMDS was also undertaken.

7.2.2. Nonmetric Multidimensional Scaling (NMDS)

NMDS, like PCoA, can create ordinations using any distance matrix but unlike PCoA, NMDS does not preserve the exact distance among sites in an ordination plot, rather it aims to represent the ordering relationship between sites in two-dimensional space. Unlike PCoA, the NMDS is not an eigenvalue technique and therefore does not require any corrections prior to analysis.

While the computations underlying NMDS are complex, the methodology is fairly straightforward:

1.) plot the distance matrix against distance in the 2D NMDS
2.) perform a non-parametric regression
3.) measure the goodness of fit of the regression by calculating the stress value
4.) perturb the existing configuration in the direction of decreasing stress
5.) repeat steps 2 to 4 until convergence is achieved

The first step then is to plot the dissimilarity measure (i.e. *Tdis* or *Rdis*) for each site pair against the actual distance between the two sites on the ordination plot (i.e. the

ordination distance), this type of plot being referred to as a Shepard diagram. A non-parametric regression line can then be fitted to the data. The distance between a point on the Shepard diagram (i.e. a site pair) and the regression line is the 'stress' for that site pair (i.e. how much the site pair has to be 'bumped from its actual position in multi-dimensional space to be represented in two dimensions. The sum of the distances of the points in a Shepard diagram is the stress of the NMDS.

It is important to run the NMDS many times starting with different random positions to be assured that the minimum stress value reached is the global minimum and not a local minimum. Therefore 100 random restarts were done for each NMDS. The final two-dimensional stress for the NMDS for each depth zone and dissimilarity measure are summarized in Table 7.2.

Table 7.2 Two dimensional stress associated with the NMDS for each depth zone using *Tdis* and *Rdis*.

Depth zone	NMDS 2D stress (*Tdis*)	NMDS 2D stress (*Rdis*)
2-5m	0.1199	0.1337
5-8m	0.1340	0.1288
8-15m	0.1331	0.1673
15-26m	0.1684	0.0986

While there is no clear rule for what level of stress is acceptable, Clarke and Warwick (2001) suggest that the interpretation of NMDS ordinations with stress values between 0.1 and 0.2 benefit from the superimposition of cluster groups. Therefore a cluster analysis was undertaken for each depth zone and dissimilarity measure (described later).

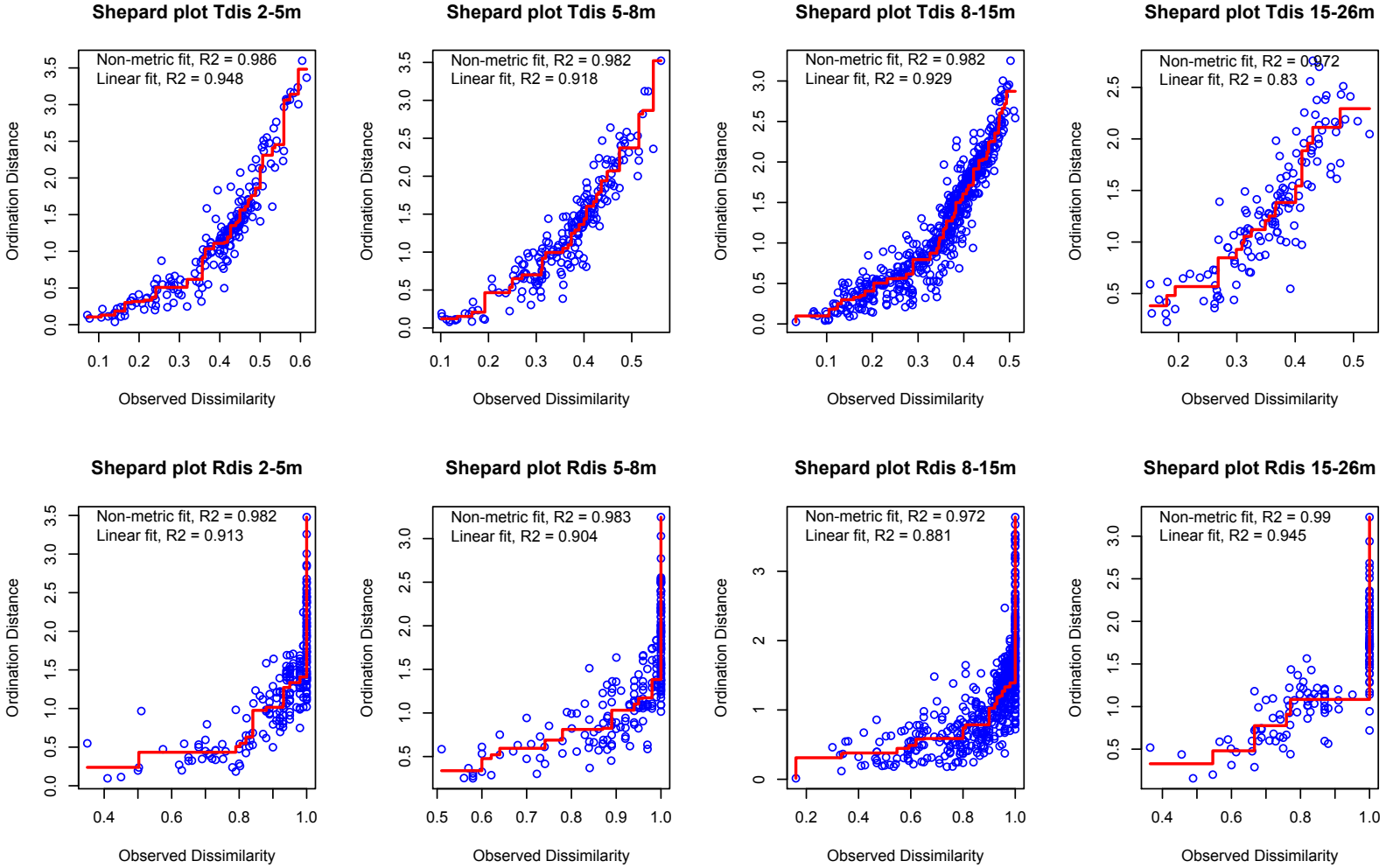

Shepard plot Tdis 2-5m
Non-metric fit, R2 = 0.986
Linear fit, R2 = 0.948
Shepard plot Tdis 5-8m
Non-metric fit, R2 = 0.982
Linear fit, R2 = 0.918
Shepard plot Tdis 8-15m
Non-metric fit, R2 = 0.982
Linear fit, R2 = 0.929
Shepard plot Tdis 15-26m
Non-metric fit, R2 = 0.972
Linear fit, R2 = 0.83
Shepard plot Rdis 2-5m
Non-metric fit, R2 = 0.982
Linear fit, R2 = 0.913
Shepard plot Rdis 5-8m
Non-metric fit, R2 = 0.983
Linear fit, R2 = 0.904
Shepard plot Rdis 8-15m
Non-metric fit, R2 = 0.972
Linear fit, R2 = 0.881
Shepard plot Rdis 15-26m
Non-metric fit, R2 = 0.99
Linear fit, R2 = 0.945
Ordination Distance
Observed Dissimilarity

Figure 7.1 Shepard diagrams for NMDS for each of the four depth zones (2 - 5 m, 5 - 8 m, 8 – 15 m, and 15 – 26 m) and dissimilarity measures (*Tdis* and *Rdis*). Note how *Rdis* (bottom row) results in many site pairs being considered completely dissimilar (i.e. reaches one on the x-axis) while *Tdis* does not consider any of the site pairs completely dissimilar in terms of the 26 traits considered. Also note that the spread about the fitted non-parametric regression line (in red) is greater for *Rdis* than for *Tdis*.

From Figure 7.1 it is clear that for the 26 life-history traits considered no two sites contain completely different trait-combinations (although some are very different). If however, a smaller number of traits were used and a few of these traits were rare it is possible that two sites could be considered completely dissimilar in terms of traits. So *Tdis* has far stricter criteria for classifying two sites as being completely dissimilar than *Rdis* and this is reflected in ordination results (which is very obvious when looking at the Shepard diagrams in Figure 7.1). Since *Tdis* has a high criteria for what qualifies as dissimilarity it could be argued that it reflects natural gradients found in ecosystems more realistically than species-overlap approaches.

In addition, looking at the goodness of fit for individual sites in the NMDS plots (Figure 7.2) it is clear that in most cases *Tdis* results in clusters of sites that are both 'tighter' and also have better goodness of fit as compared to *Rdis*. The goodness of fit was implemented using the **goodness ()** function in the **vegan** package in R.

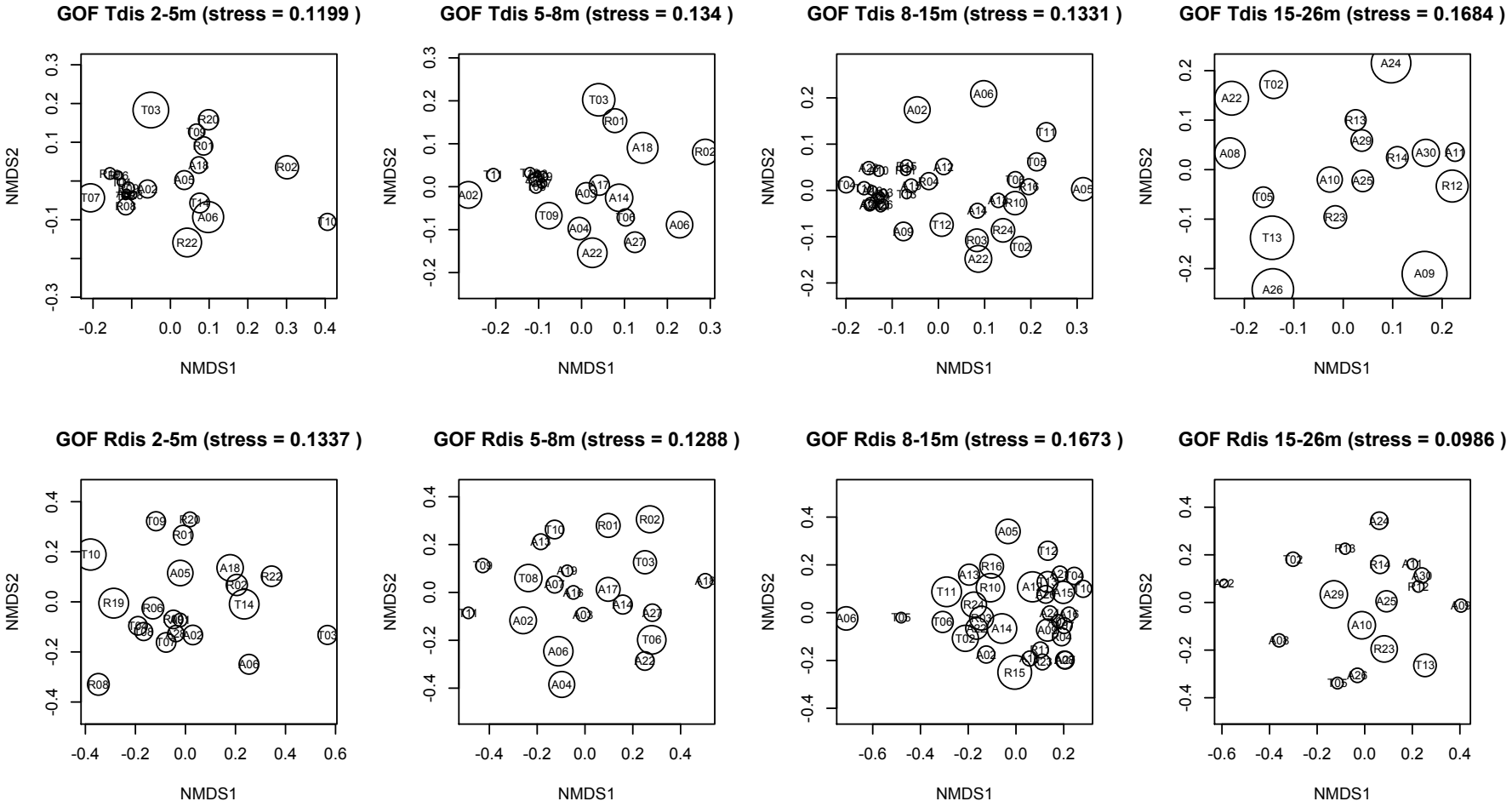

GOF Tdis 2-5m (stress = 0.1199)
GOF Tdis 5-8m (stress = 0.134)
GOF Tdis 8-15m (stress = 0.1331)
GOF Tdis 15-26m (stress = 0.1684)
GOF Rdis 2-5m (stress = 0.1337)
GOF Rdis 5-8m (stress = 0.1288)
GOF Rdis 8-15m (stress = 0.1673)
GOF Rdis 15-26m (stress = 0.0986)
NMDS1
NMDS2

Figure 7.2 Goodness of fit for the NMDS plots based on *Tdis* (top row) and *Rdis* (bottom row). Note that *Tdis* was able to achieve far better fits for tight clusters of sites.

7.2.3. Clustering methodology

As recommended by Clarke and Warwick (2001) cluster groups were superimposed on the NMDS ordinations since most had stress values between 0.1 and 0.2. Therefore a cluster analysis was undertaken for each depth zone and dissimilarity.

The most appropriate clustering method was found by calculating the cophenetic correlations (namely the Pearson's r correlation between the original dissimilarity matrix and a matrix of 'joining distances' from the dendrogram) of several clustering methods for each dissimilarity matrix (methodology detailed in Chapter Six section 6.2.4.1). The unweighted pair-groups method using arithmetic averages (UPGMA) or 'average' clustering was found to be the most appropriate (i.e. produced the highest cophenetic correlation scores) and was therefore used.

The selection of the most appropriate number of clusters to extract from the resulting dendrograms (i.e. cutting level) were determined using a number of tools including silhouette plots, goodness of fit plots, and cluster fusion diagrams (the methodology and interpretation of such quality control tests are detailed in Chapter Six). To emphasize how ordination structures were largely similar for *Tdis* and *Rdis* at higher levels of dissimilarity but differed at lower levels of dissimilarity, two cutting levels were selected for each dendrogram (for example, see red and blue horizontal lines in dendrograms in Figure 7.3)

The cophenetic correlations for resulting from UPGMA clustering and the number of groups selected based on the fusion levels and silhouette plots are summarized in Table 7.3.

Table 7.3 Cophenetic correlation for the dissimilarity matrices for each depth zone using UPGMA as the clustering method.

Depth zone	Cophenetic correlation (*Tdis*)	Upper cut	Lower cut	Cophenetic correlation (*Rdis)*	Upper cut	Lower cut
2-5m	0.943	0.42	0.2	0.859	0.95	0.8
5-8m	0.843	0.38	0.2	0.769	0.93	0.81
8-15m	0.908	0.35	0.25	0.835	0.93	0.61
15-26m	0.76	0.36	0.25	0.715	0.86	0.73

The cophenetic correlations were high indicating that the UPGMA clustering methodology produced dendrograms representative of the original distance matrix. Note that for each depth range a more representative dendrogram was produced using *Tdis* rather than *Rdis* and also that groups could be identified at much lower levels of dissimilarity. This is due to the many site pairs that *Rdis* considers completely dissimilarity (i.e. no overlapping species). *Tdis* however does not have this large group of completely dissimilar sites (see sites-pairs at dissimilarity 1 in Shepard diagrams; Figure 7.1) therefore a more 'fine-tuned' dendrogram can be achieved.

7.3. Results

For clarity the results are presented as follows. First the large-scale structures of the dendrograms, PCOAs and NMDSs resulting from using *Tdis* and *Rdis* are compared side by side for each depth zone (Figure 7.3 to Figure 7.9). Clusters resulting from cutting the dendrogram at a medium to high level of dissimilarity are shown in all figures as a red line while clustering results from cutting the dendrogram at a lower level of dissimilarity is shown in all figures as a blue line. The cutting levels for the higher and lower level clustering for each depth zone are shown in Table 7.3.

Second, results from overlaying the environmental variables onto the *Rdis* and *Tdis* NMDS plots are presented (Figure 7.12 to Figure 7.19). Here *Rdis* and *Tdis* are compared in terms of how their resulting structures relate to environmental variables. Since NMDS is a purely descriptive tool no attempt can or is made to determine the statistical significance of relationships between specific ordination structures (i.e. clusters) and environmental variables. Instead the plots are discussed more generally in terms of differences in the interpretations that the ordinations imply.

Finally, the differences between *Tdis* and *Rdis* in terms of the resulting smaller scale ordination structures are demonstrated by focusing on the movement of sites within one particular large-scale structure at one particular depth zone as one moves from a *Rdis* to *Tdis*-based ordination Figure 7.20 to Figure 7.22. The coral compositions of the sites within this large-scale cluster are discussed in detail and used as a tool for highlighting the advantages of using *Tdis* over *Rdis*.

The overall question of whether *Tdis* is a more useful for ordination than *Rdis* along with advantages and disadvantages of both is addressed in the discussion section.

7.3.1. Large-scale difference between Rdis and Tdis-based ordinations

Figure 7.3, Figure 7.5, Figure 7.7, and Figure 7.9 show how the UPGMA hierarchical clustering, the PCoA and the NMDS differed when using *Rdis* and *Tdis*. Two separate cutting levels for each dendrogram (red and blue horizontal lines on dendrograms) are shown to emphasize differences between *Tdis* and *Rdis* in terms of higher and lower level clustering. The site clusters or groups that result from cutting the dendrograms are superimposed on the PCoA and NMDS plots as coloured contours.

Figure 7.4, Figure 7.6, Figure 7.8, and Figure 7.10 show the large-scale clusters resulting from the *Tdis* and *Rdis*-based UPGMA hierarchical clustering overlaid onto maps of the three study regions (Andavadoaka, Ranobe, and Tulear). These figures show the large-scale differences between *Rdis* and *Tdis*-based ordination in terms of the actual geographical locations of the reef sites.

The large-scale differences between the results based on *Rdis* and those based on *Tdis* are:

1. For hierarchical clustering *Tdis* results in clusters with much lower dissimilarities than *Rdis*
2. In all cases the PCoAs based on *Tdis* had lower 2-D stress than those based on *Rdis*
3. Higher level clustering structures (red lines) in dendrograms, PCoAs, and NMDSs using *Rdis* and *Tdis* are in most cases relatively similar
4. Lower level clustering structures (blue lines) in dendrograms, PCoAs, and NMDS using *Rdis* and *Tdis* are sometimes very different.

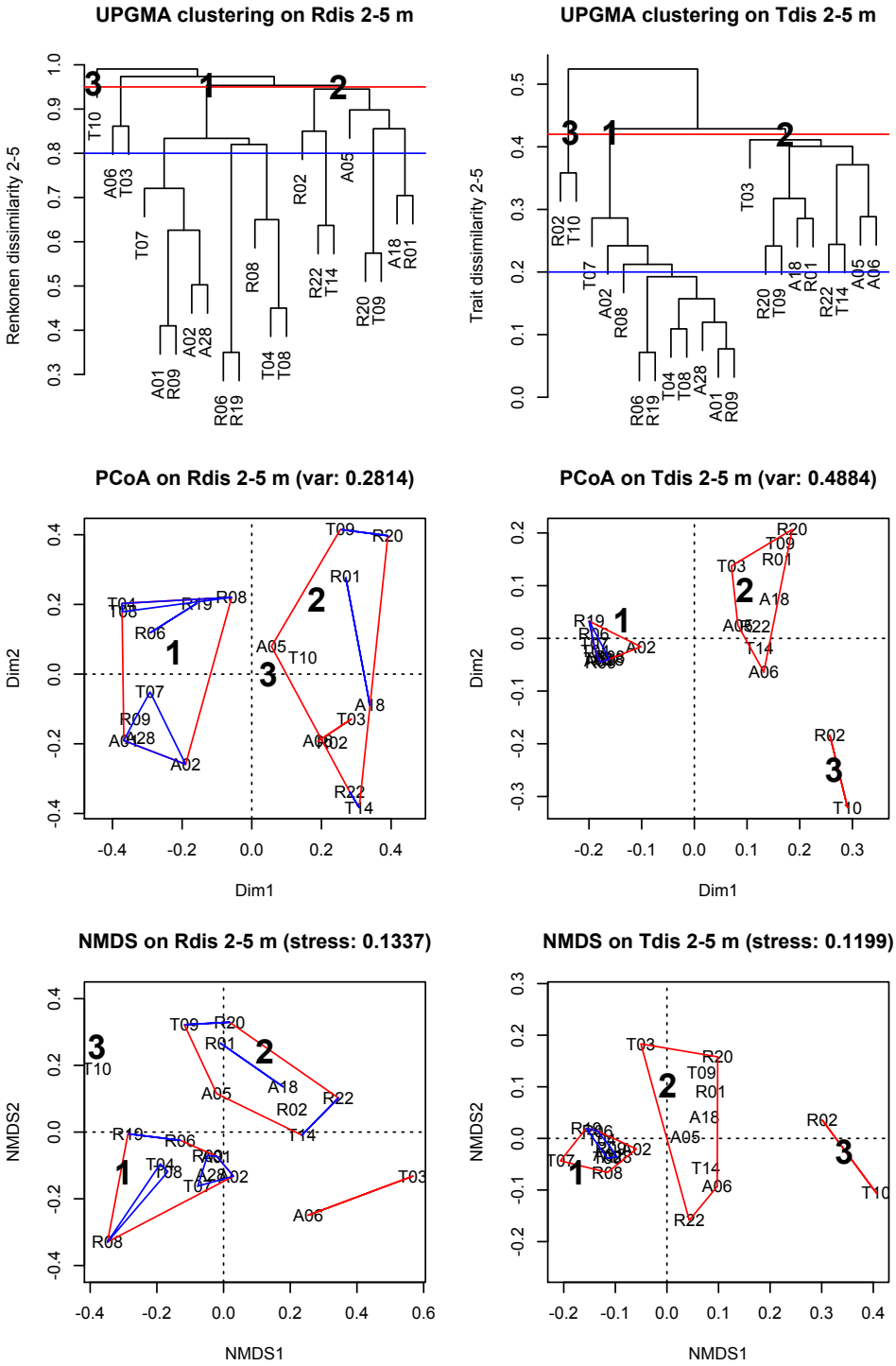
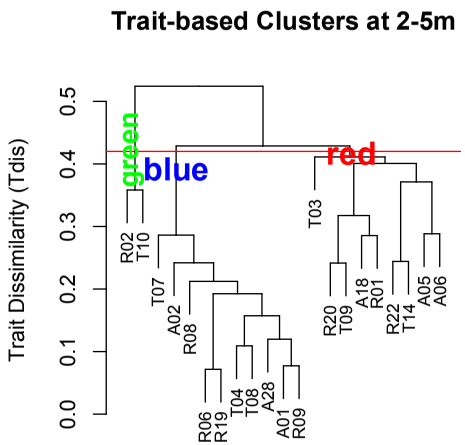
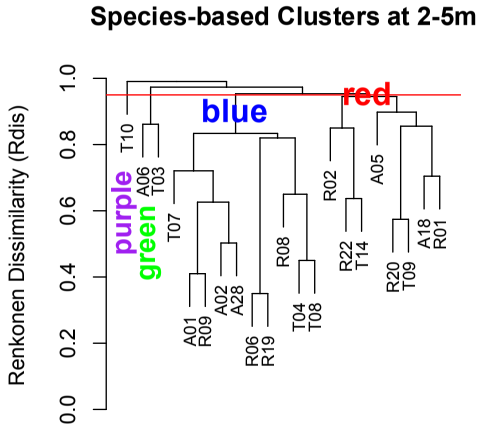
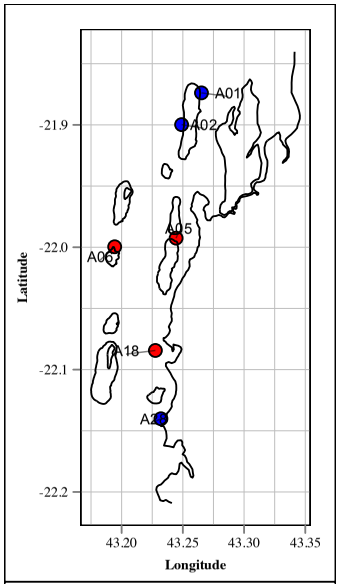


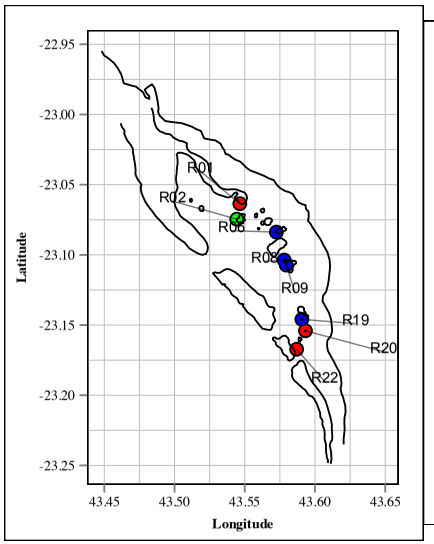
Figure 7.3 UPGMA clustering (top), PCoA (middle), and NMDS (bottom) comparison between using *Rdis* (left) and *Tdis* (right) for reef sites at two to five metres depth. Note how *Tdis* creates tighter more clear clusters at lower levels of dissimilarity (blue line) for all three analyses. Red and blue lines in the PCoA and NMDS plots reflect the site clusters resulting from cutting the dendrograms as shown in the top row.

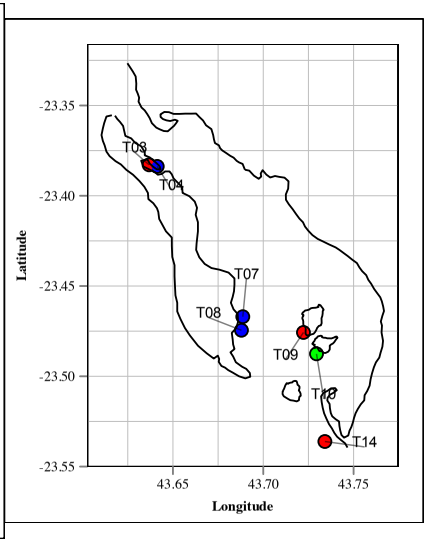
Figure 7.4 Left: Dendrograms resulting from UPGMA clustering based on *Tdis* (top) and (bottom) for reef site at the two to five metre depth zone. The red horizontal lines indicate where the dissimilarity dendrograms were cut (*Tdis* = 0.42 and *Rdis* = 0.95). The resulting site clusters are indicated on the dendrograms by coloured words. The maps to the right of the dendrograms show the locations of the sites with point colour indicating cluster membership. Maps for both the top and bottom row, going from left to right represent: Andavadoaka, Ranobe, and Tulear.

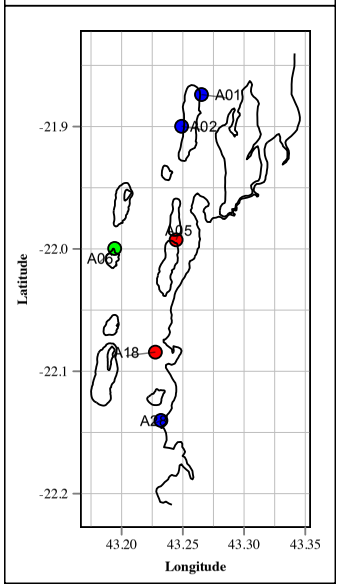

Trait-based Clusters at 2-5m
Trait Dissimilarity (Tdis)
0.0
0.1
0.2
0.3
0.4
0.5
green
blue
red
R02
T10
T07
A02
R08
R06
R19
T04
T08
A28
A01
R09
T03
R20
T09
A18
R01
R22
T14
A05
A06

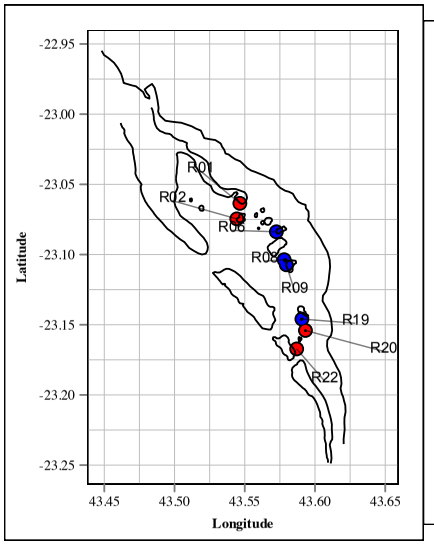

Species-based Clusters at 2-5m
Renkonen Dissimilarity (Rdis)
0.0
0.2
0.4
0.6
0.8
1.0
blue
red
purple
green
T10
A06
T03
T07
A01
R09
A02
A28
R06
R19
R08
T04
T08
R02
R22
T14
A05
R20
T09
A18
R01

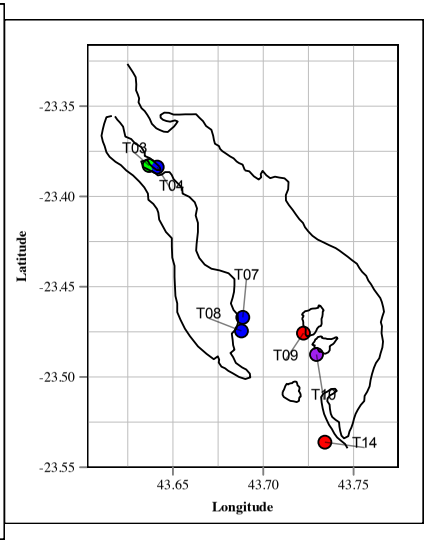

A01
A02
A05
A06
A18
A28
-21.9
-22.0
-22.1
-22.2
Latitude
43.20
43.25
43.30
43.35
Longitude


R01
R02
R06
R08
R09
R19
R20
R22
-22.95
-23.00
-23.05
-23.10
-23.15
-23.20
-23.25
Latitude
43.45
43.50
43.55
43.60
43.65
Longitude


T03
T04
T07
T08
T09
T14
-23.35
-23.40
-23.45
-23.50
-23.55
Latitude
43.65
43.70
43.75
Longitude


A01
A02
A05
A06
A18
A28
-21.9
-22.0
-22.1
-22.2
Latitude
43.20
43.25
43.30
43.35
Longitude


R01
R02
R06
R08
R09
R19
R20
R22
-22.95
-23.00
-23.05
-23.10
-23.15
-23.20
-23.25
Latitude
43.45
43.50
43.55
43.60
43.65
Longitude


T03
T04
T07
T08
T09
T14
-23.35
-23.40
-23.45
-23.50
-23.55
Latitude
43.65
43.70
43.75
Longitude

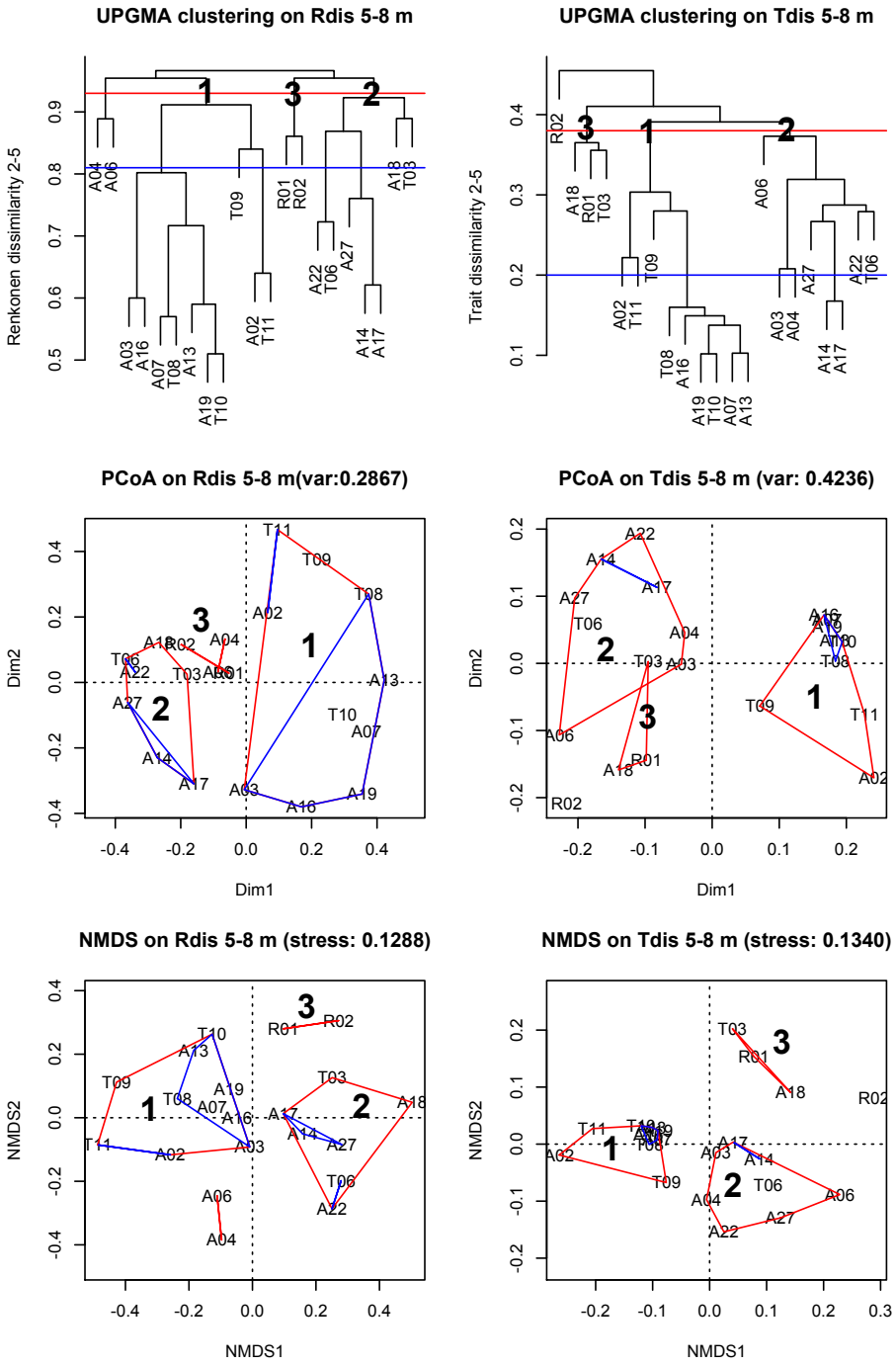
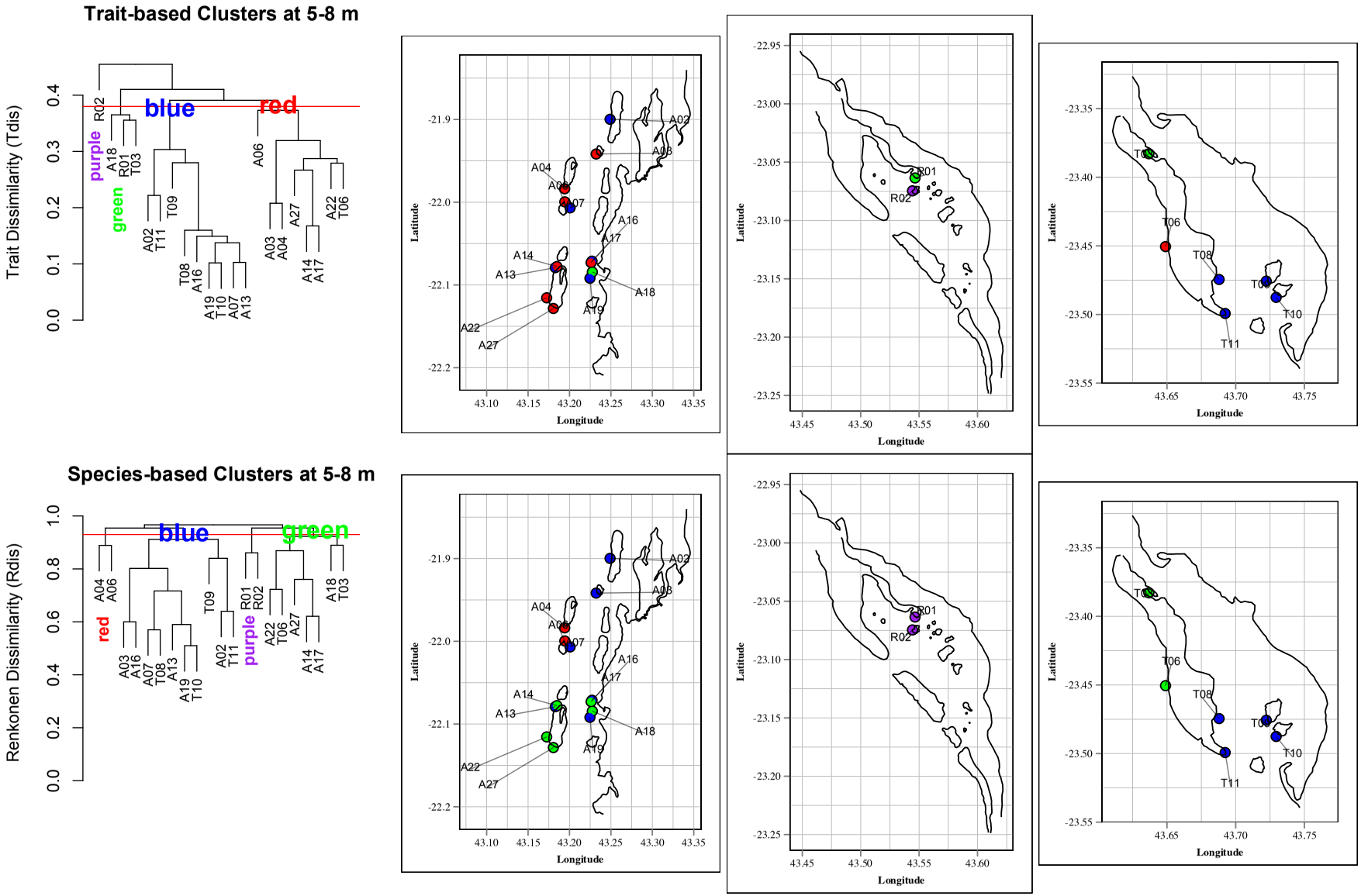


Figure 7.5 UPGMA clustering (top), PCoA (middle), and NMDS (bottom) comparison between using *Rdis* (left) and *Tdis* (right) for reef sites at five to eight metres depth. Note how *Tdis* creates tighter more clear clusters at lower levels of dissimilarity (blue line) for all three analyses. Red and blue lines in the PCoA and NMDS plots reflect the site clusters resulting from cutting the dendrogram as shown in the top row.

Figure 7.6 Left: Dendrograms resulting from UPGMA clustering based on *Tdis* (top) and *Rdis* (bottom) for reef site at five to eight metres depth. The red horizontal lines indicate where the dissimilarity dendrograms were cut (*Tdis* = 0.38 and *Rdis* = 0.93). The resulting site clusters are indicated on the dendrograms by coloured words. The maps to the right of the dendrograms show the locations of the sites with point colour indicating cluster membership. Maps for both the top and bottom row, going from left to right represent: Andavadoaka, Ranobe, and Tulear.


Trait-based Clusters at 5-8 m
Trait Dissimilarity (Tdis)
0.0
0.1
0.2
0.3
0.4
blue
red
purple
green
R02
A18
R01
T03
A02
T11
T09
T08
A16
A19
T10
A07
A13
A06
A03
A04
A27
A14
A17
A22
T06
Species-based Clusters at 5-8 m
Renkonen Dissimilarity (Rdis)
0.0
0.2
0.4
0.6
0.8
1.0
blue
green
red
purple
A04
A06
A03
A16
A07
T08
A13
A19
T10
T09
A02
T11
R01
R02
A22
T06
A27
A14
A17
A18
T03
Latitude
Longitude
-21.9
-22.0
-22.1
-22.2
43.10
43.15
43.20
43.25
43.30
43.35
A02
A03
A04
A06
A07
A16
A17
A14
A13
A18
A19
A22
A27
-22.95
-23.00
-23.05
-23.10
-23.15
-23.20
-23.25
43.45
43.50
43.55
43.60
R01
R02
-23.35
-23.40
-23.45
-23.50
-23.55
43.65
43.70
43.75
T06
T08
T10
T11

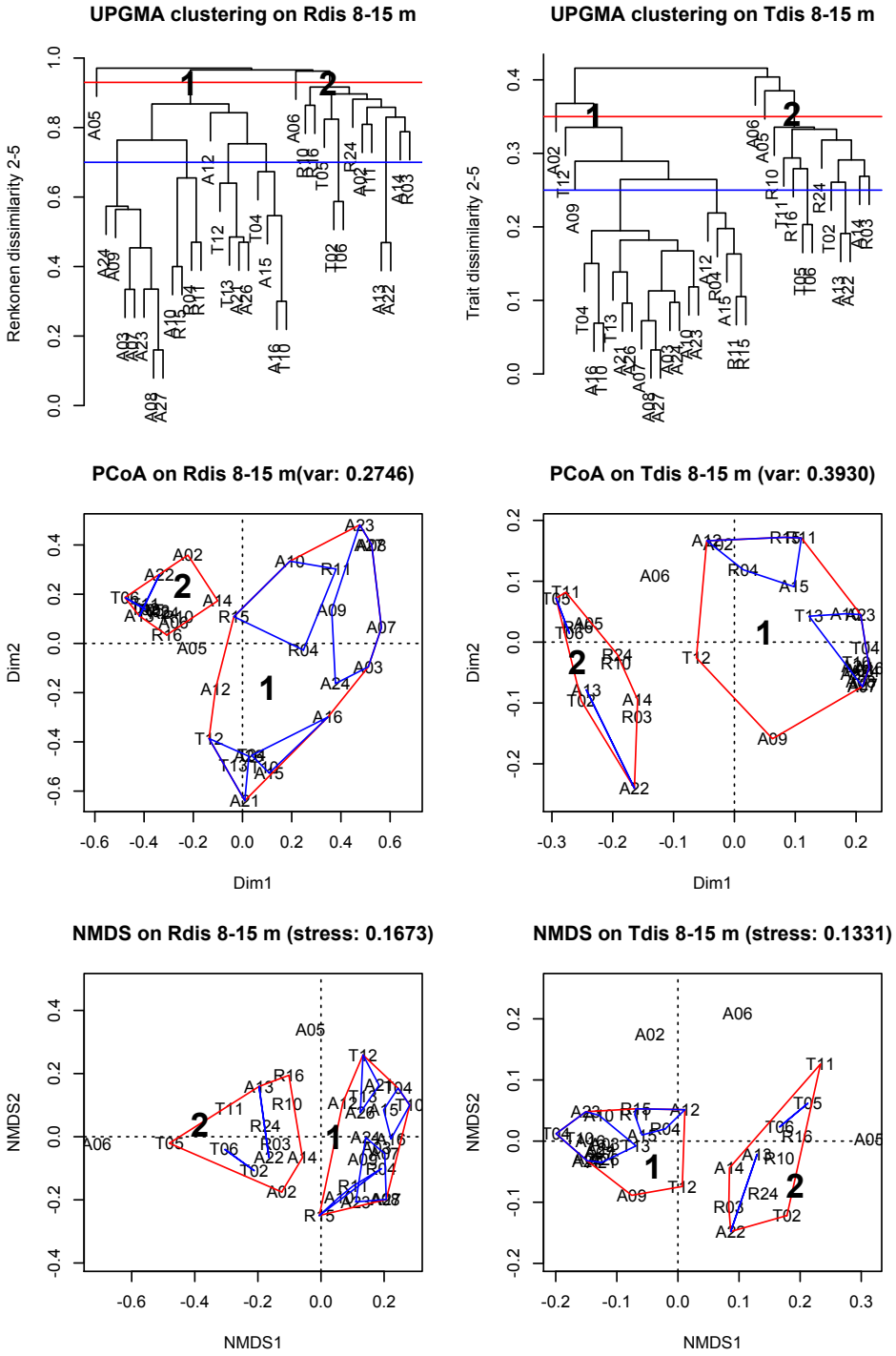
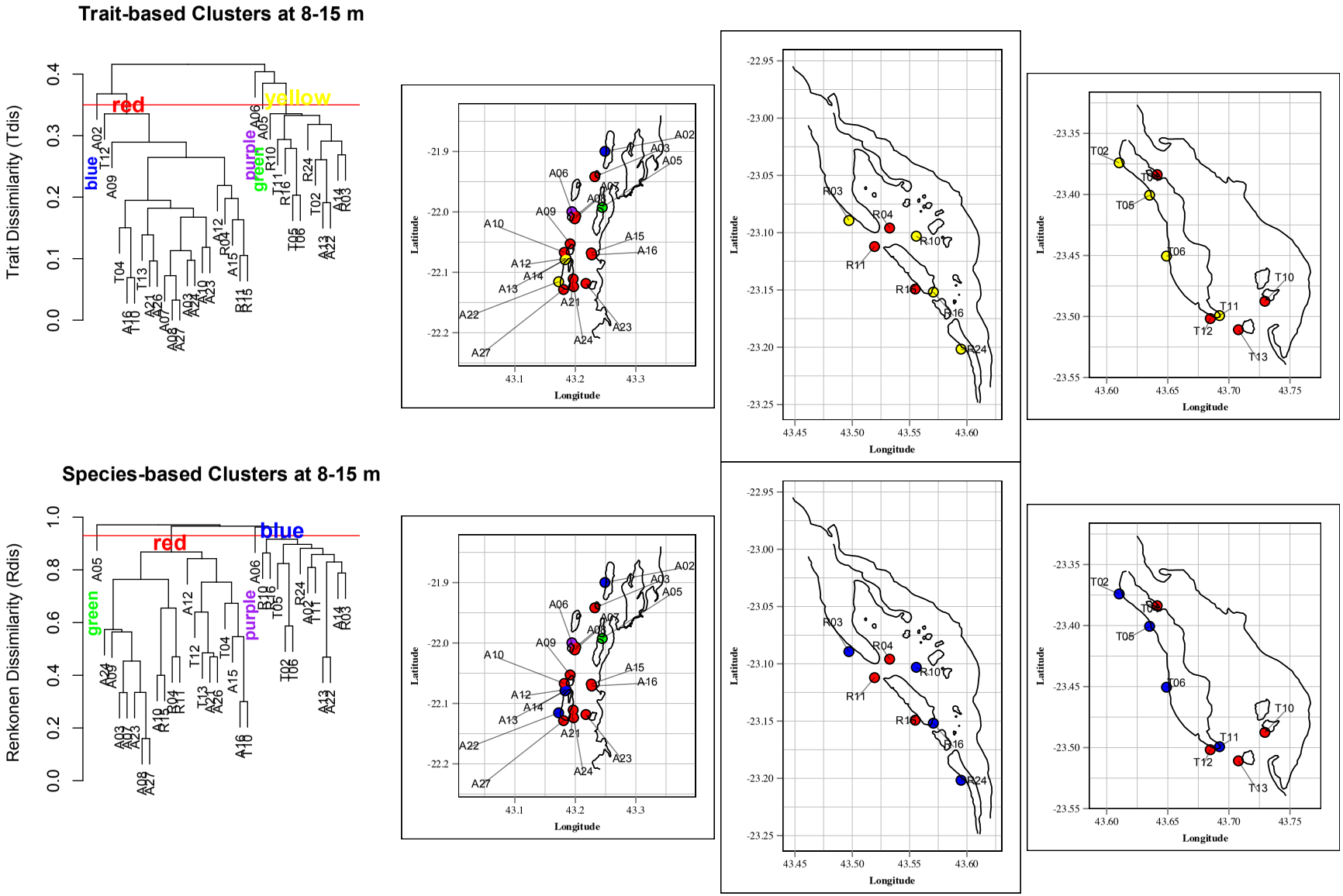


Figure 7.7 UPGMA clustering (top), PCoA (middle), and NMDS (bottom) comparison between using *Rdis* (left) and *Tdis* (right) for reef sites at eight to 15 metres depth. Note how *Tdis* creates tighter more clear clusters at lower levels of dissimilarity (blue line) for all three analyses. Red and blue lines in the PCoA and NMDS plots reflect the site clusters resulting from cutting the dendrogram as shown in the top row.

Figure 7.8 Left: Dendrograms resulting from UPGMA clustering based on *Tdis* (top) and *Rdis* (bottom) for reef site at the eight to 15 metre depth zone. The red horizontal lines indicate where the dissimilarity dendrograms were cut (*Tdis* = 0.35 and *Rdis* = 0.93). The resulting site clusters are indicated on the dendrograms by coloured words. The maps to the right of the dendrograms show the locations of the sites with point colour indicating cluster membership. Maps for both the top and bottom row, going from left to right represent: Andavadoaka, Ranobe, and Tulear.


Trait-based Clusters at 8-15 m
Trait Dissimilarity (Tdis)
red
yellow
blue
purple
green
Species-based Clusters at 8-15 m
Renkonen Dissimilarity (Rdis)
Latitude
Longitude

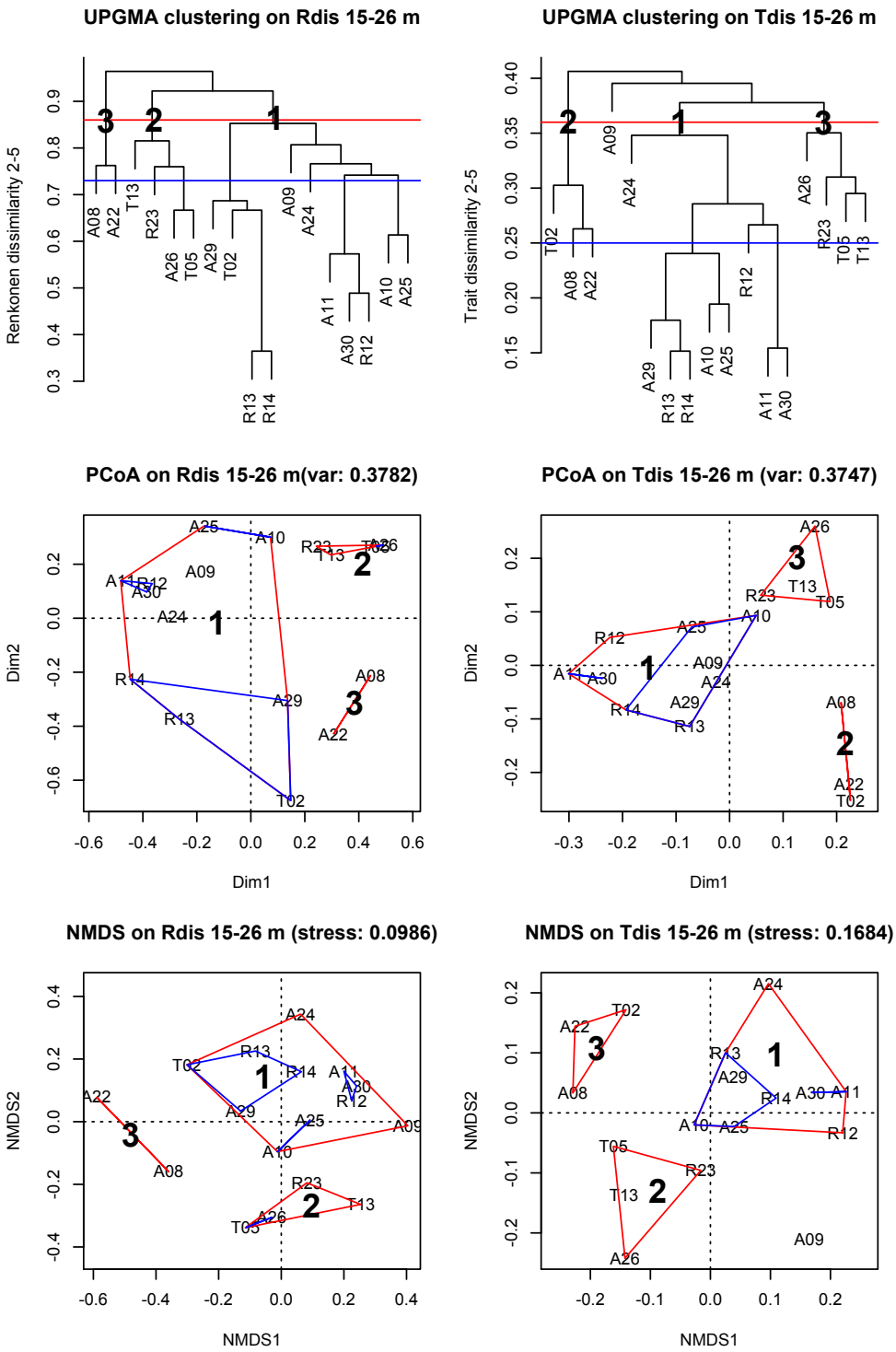
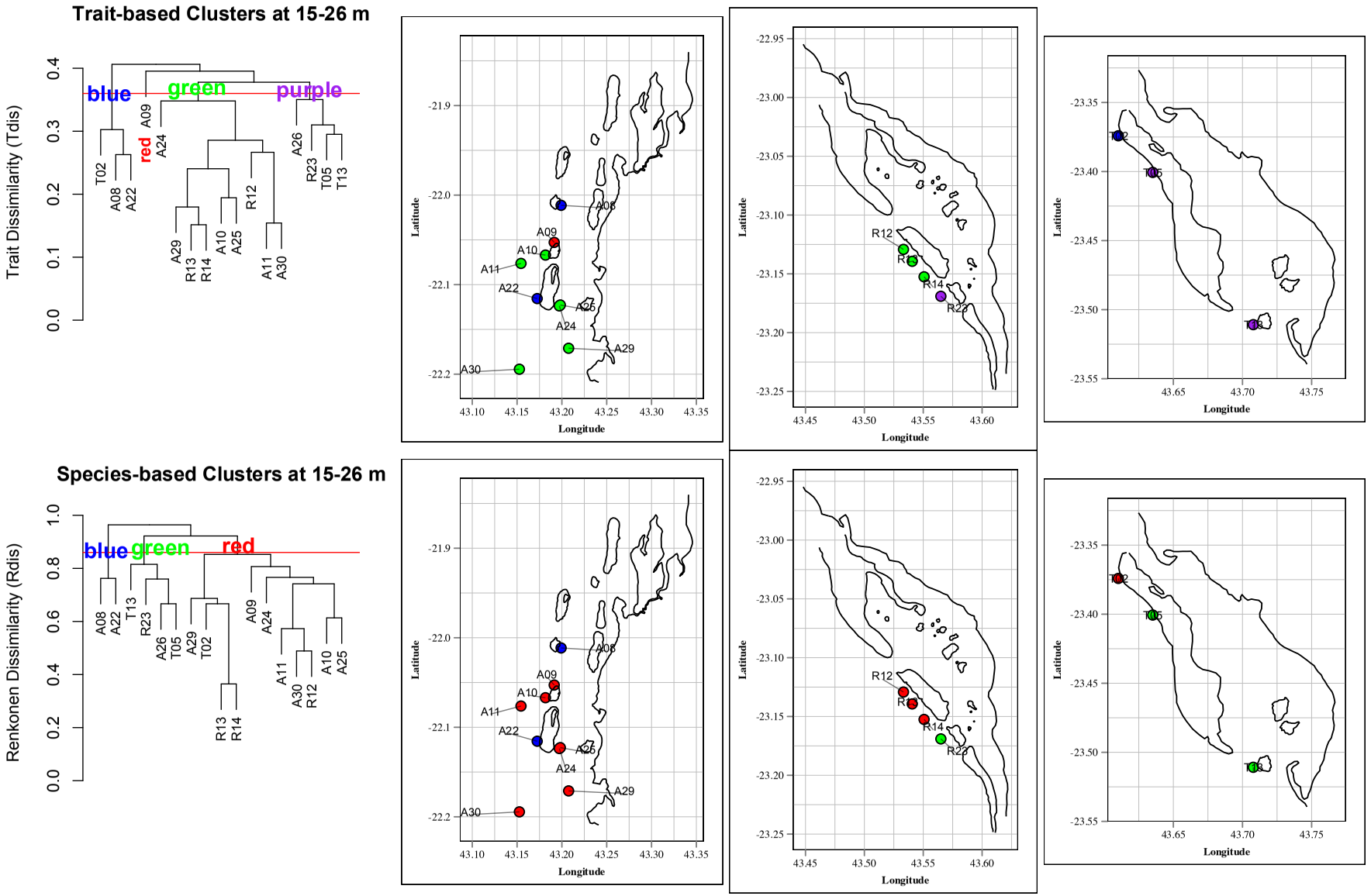


Figure 7.9 UPGMA clustering (top), PCoA (middle), and NMDS (bottom) comparison between using *Rdis* (left) and *Tdis* (right) for reef sites at 15 to 26 metres depth. Note how *Tdis* creates tighter more clear clusters at lower levels of dissimilarity (blue line) for all three analyses. Red and blue lines in the PCoA and NMDS plots reflect the site clusters resulting from cutting the dendrogram as shown in the top row.

Figure 7.10 Left: Dendrograms resulting from UPGMA clustering based on *Tdis* (top) and *Rdis* (bottom) for reef site at the 15 to 26 metre depth zone. The red horizontal lines indicate where the dissimilarity dendrograms were cut (*Tdis* = 0.36 and *Rdis* = 0.86). The resulting site clusters are indicated on the dendrograms by coloured words. The maps to the right of the dendrograms show the locations of the sites with point colour indicating cluster membership. Maps for both the top and bottom row, going from left to right represent: Andavadoaka, Ranobe, and Tulear.


Trait-based Clusters at 15-26 m
Trait Dissimilarity (Tdis)
0.0
0.1
0.2
0.3
0.4
blue
green
purple
red
T02
A08
A22
A09
A24
A29
R13
R14
A10
A25
R12
A11
A30
A26
R23
T05
T13
Species-based Clusters at 15-26 m
Renkonen Dissimilarity (Rdis)
0.0
0.2
0.4
0.6
0.8
1.0
blue
green
red
A08
A22
T13
R23
A26
T05
A29
T02
R13
R14
A09
A24
A11
A30
R12
A10
A25
Latitude
Longitude
-21.9
-22.0
-22.1
-22.2
43.10
43.15
43.20
43.25
43.30
43.35
-22.95
-23.00
-23.05
-23.10
-23.15
-23.20
-23.25
43.45
43.50
43.55
43.60
-23.35
-23.40
-23.45
-23.50
-23.55
43.65
43.70
43.75

Overall the PCoAs and NMDSs had similar structures, which was reassuring, however, the amount of variance that the *Rdis*-based PCOA was able to capture was rather low (the first two eigenvalues explained only 27 to 28 percent of the total variation in the dataset for all depth zones). Therefore NMDS plots are used from this point forward to discuss details of observed differences between and *Tdis*-based plots.

7.3.2. Large-scale ordination differences and environmental variables

7.3.2.1. Environmental variables

The three environmental variables considered for each reef site in this study are: distance (in km) to nearest seaward object (fetch), distance (in km) to nearest river mouth, and number of Vezo fishing huts within a ten kilometre radius. A fourth pseudo 'environmental variable' is reef type (detailed in Chapter Four).

Fetch and distance to river mouth were incorporated as both continuous and categorical variables. The 'distance to nearest seaward object' for reef sites outside the barrier reef was nearly 800 km (the distance to the coast of Mozambique) whilst for reef sites inside the barrier the distances ranged between 0.1 and 4.44 km). Because of this large gap between distances it was decided that fetch was best treated as a categorical variable. Reef type was only considered as a categorical variable.

Figure 7.11 shows the 'breaks' in the continuous environmental data for the reef sites and how these were used to impose the categorical variables.

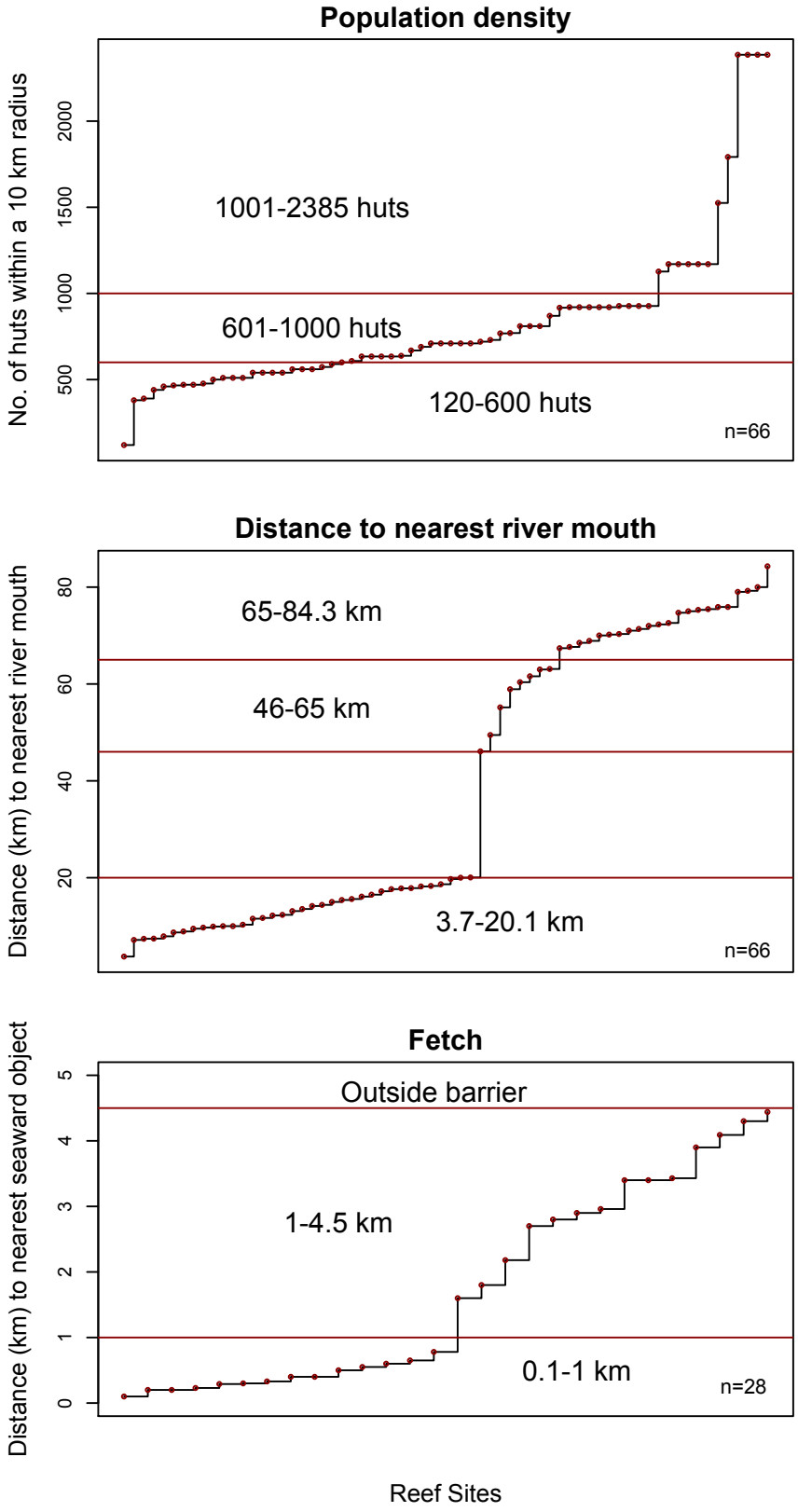


Figure 7.11 Division in the continuity of the environmental variables for the reef sites. Red lines and labels indicate how the divisions were used to establish categorical variables for the data.

For each depth zone two figures are presented. The first figure compares the *Rdis* and *Tdis*-based NMDS plots with reef type and distance to nearest seaward object (fetch) overlaid (Figure 7.12, Figure 7.14, Figure 7.16 and Figure 7.18). The second figure compares the *Rdis* and *Tdis*-based NMDS plots with distance to nearest river mouth (sedimentation) and fishermen population density (huts within a ten km radius of site) overlaid (Figure 7.13, Figure 7.15, Figure 7.17, and Figure 7.19).

Distance to river mouth and number of huts within a ten km radius were added to the NMDS plots as vectors using the **envfit()** function of the vegan package in R and also categorically via use of colours and symbols (Figure 7.13 to Figure 7.19). The **envfit()** functions finds vectors or factor averages of continuous environmental variables and adds them to an ordination diagram such that the projection of reef sites onto environmental vectors have the maximum correlation possible. Arrow length indicates the strength of the correlation; short arrows represent weaker correlations while longer arrows represent stronger correlations.

The movement of reef sites from their position in the *Rdis*-based NMDS to their position in the *Tdis*-based NMDS is shown in Figure 7.13 to Figure 7.19 by the dashed arrows in the *Rdis*-based NMDS (top plot) in each figure. Only sites that move in or out the large-scale clusters (shown as red contours) are indicated with dashed arrows and clusters that merge are indicated with a double-headed arrow. The large-scale movement of sites going from the *Rdis*-NMDS to the *Tdis*-NMDS highlights sites that are functionally very poorly placed, that is, they are placed into a cluster because of low-levels of species overlap when in fact they have high levels of trait-combination overlap with a different cluster.

Smaller-scale movement also occurs within the large-scale clusters (NB movement of sites between the clusters is indicated by blue contours). This smaller-scale movement represents a fine-tuning of the sites while large-scale movement shows sites that are misplaced in terms of functionality by the *Rdis*-based NMDS.

7.3.2.2. NMDS plots with Environmental variables at 2-5m

Large-scale movement of sites when going from *Rdis* to *Tdis* at the two to five metre depth zone consisted of: 1) R02 moving from Cluster Two in the *Rdis*-based NMDS to form Cluster Three with T10 in the *Tdis*-based NMDS and 2) the merging of A06 and T03 with Cluster Two (these movements are summarized in the top plot of Figure 7.12). The appropriateness of each move is now discussed.

R02 was moved from Cluster Two to form Cluster Three with site T10 when using *Tdis*. This is more appropriate than the position R02 held in Cluster Two since R02 contain 41 percent *Fungia spp*. which matches up with the nearly 47 percent *Cycloseris spp.* at site T10. This clustering also makes more ecological sense as T10 and R02 both are MMR reef located inside the barrier with one to 4.5 kilometres distance to the nearest seaward object, are within 20 km of a river mouth, and have similar levels of fishermen populations. This is more appropriate than keeping R02 in Cluster Two as none of the sites in Cluster Two contained small free-living corals in such abundance.

Merging A06 and T03 with *Tdis* Cluster Two was also appropriate. *Rdis* matched A06 and T03 based on a 14 percent overlap in species composition of massive Porites species (*P. solida, P. lutea,* and *P. lobata*). The ignored species that dominated the remainder for A06 were *Leptoseris incrustance* (37 percent) and *Pocillopora damicornis* (39 percent) and for T03 large monostands of *Porites rus* were dominant (69 percent). Based on the composition of the remainders of both A06 and T03 they are both better placed in Cluster Two, which contains sites with species from the emergent groups *Pocilloporidae*, *Leptastrea*, and *Porites*.

The merge described above did not greatly change the self-similarity of Cluster Two in terms of environmental variables. For both *Rdis* and *Tdis* Cluster Two contained mostly MMR reefs, within 20 km of a river mouth, with varying levels of fetch and fishing intensity.

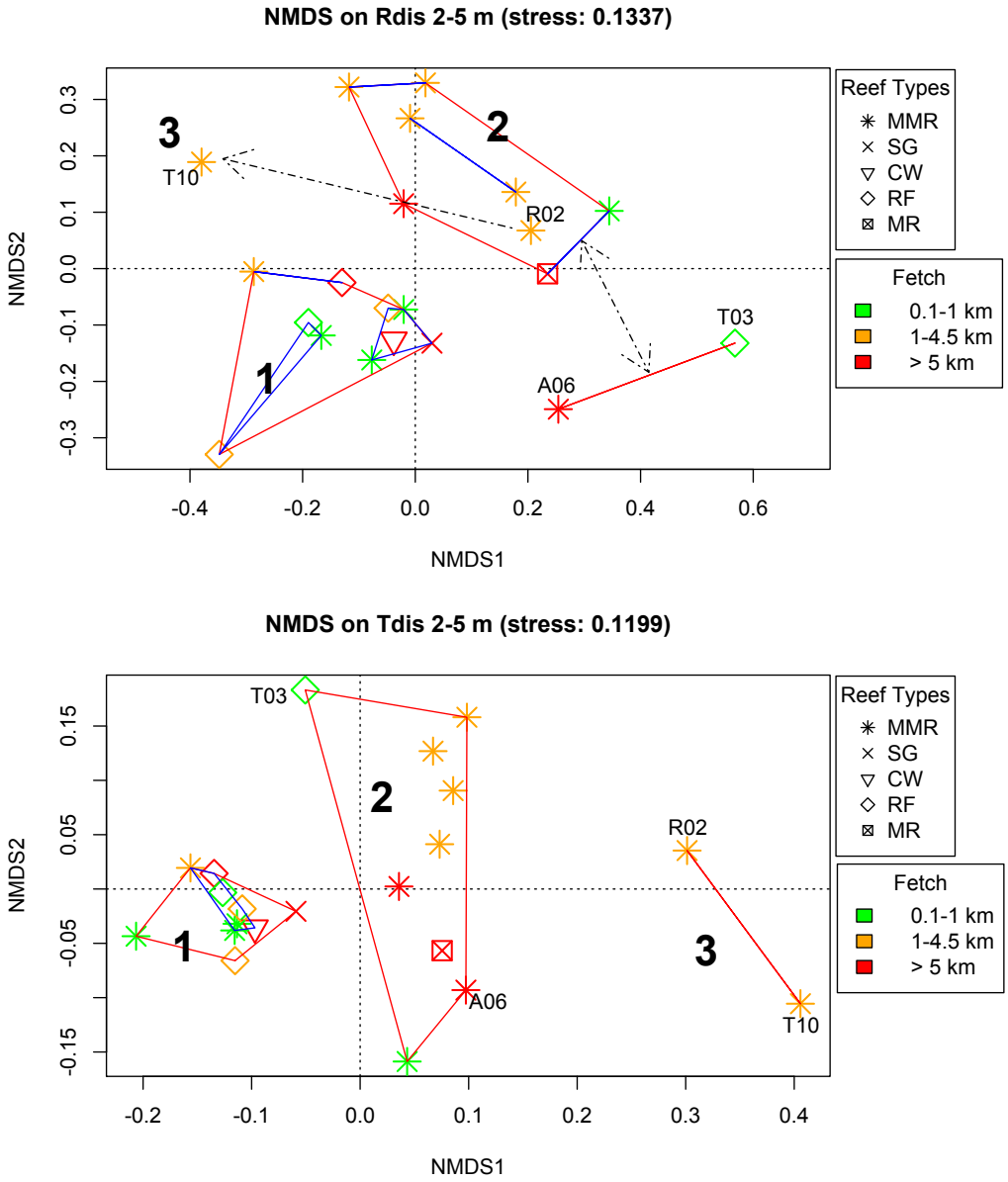


Figure 7.12 Comparison between an *Rdis*-based (top) NMDS and *Tdis*-based (bottom) NMDS for sites at two to five metres depth. Reef types are indicated by symbols. The higher level clusters are shown in red and the lower level cluster are shown as blue contours. The cutting levels are the same as in Figure 7.3.

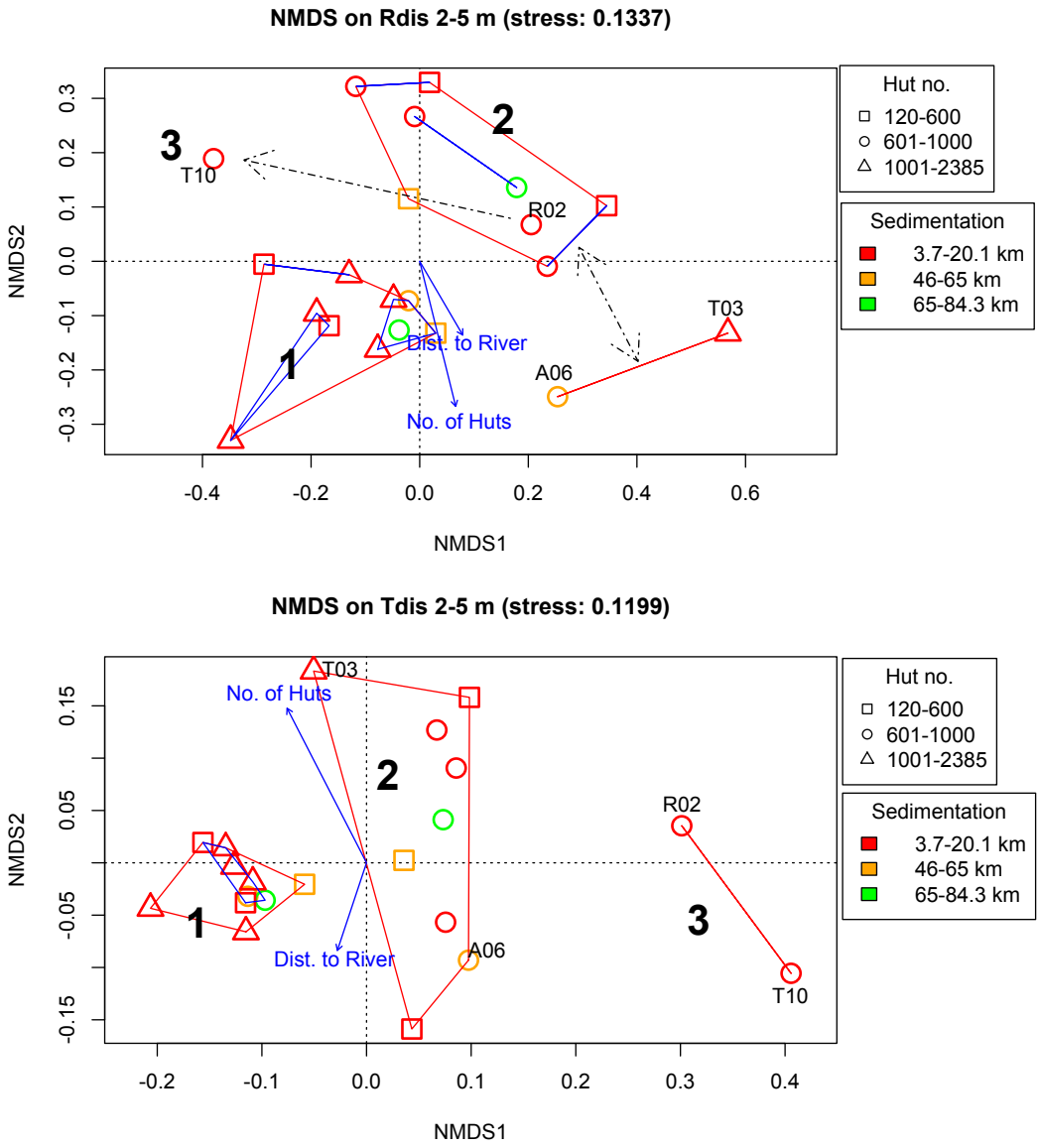


Figure 7.13 Comparison between an *Rdis*-based (top) NMDS and *Tdis*-based (bottom) NMDS for sites at at two to five metres depth. Environmental vectors (no. of huts and distance to nearest river mouth) for the ordination are show as blue arrows. The higher level clusters are shown in red and the lower level cluster are shown as blue contours. The cutting levels are the same as in Figure 7.3.

7.3.2.3. NMDS plots with Environmental variables at 5-8 m

The large-scale movement of sites when going from *Rdis* to *Tdis*-based NMDS plots at five to eight metres depth were as follows: A06 and A04 moved from a separate cluster into Cluster Two, A03 moved from Cluster One to Cluster Two, T03 and A18 moved from Cluster Two to Cluster Three and R02 moved out of Cluster Three (the dashed arrows in the top plot of Figure 7.14 summarizes these movements). Overall this movement resulted in nearly all reefs with high fetch being placed in Cluster Two and a tight cluster of patch reefs with mounds (M) or mounds, mono-stands, and rubble zones (MMR) within Cluster One.

Cluster One was largely dominated by *Acropora* and *Isopora*. While A03 did contain nearly 41 percent *Acropora* species (NB this does not imply 41 percent overlap with other *Acropora* species in the cluster) the remainder contained 25 percent *Galaxea fasicularis*, 20 percent *Echinopora hisutissima*, and 14 percent *Favites pentagona*. This composition fit better in with the structurally robust and fetch-adapted composition of sites in Cluster Two which contained mostly the emergent groups *Pocilloporidae* and *Porites* massive, and also *Leptastrea* spp., *Favites* spp., *Echinopora hirsutissima*, *Goniastrea edwardsi*, *Coscinarea columna*, *Montastrea* spp., *Pavona varians*, and *Platygyra* spp.

Site A04 and A06 which were matched up in the *Rdis* based NMDS plot based on an 11 percent overlap in *Echinopora hirsutissima* also fit better into Cluster Two as their remainder compositions contained only species from those listed above.

Site T03 and A18 were moved from Cluster Two in the *Rdis*-based NMDS to form Cluster Three with R01 in the *Tdis*-based NMDS. These sites had diverse non-*Acropora* communities. Site R02 was identified as an outlier by *Tdis* due largely to the composition consisting of 25 percent *Plerogyra sinuosa* and 14 percent *Lobophyllia hemprichii*; two species with quite unique traits sets.

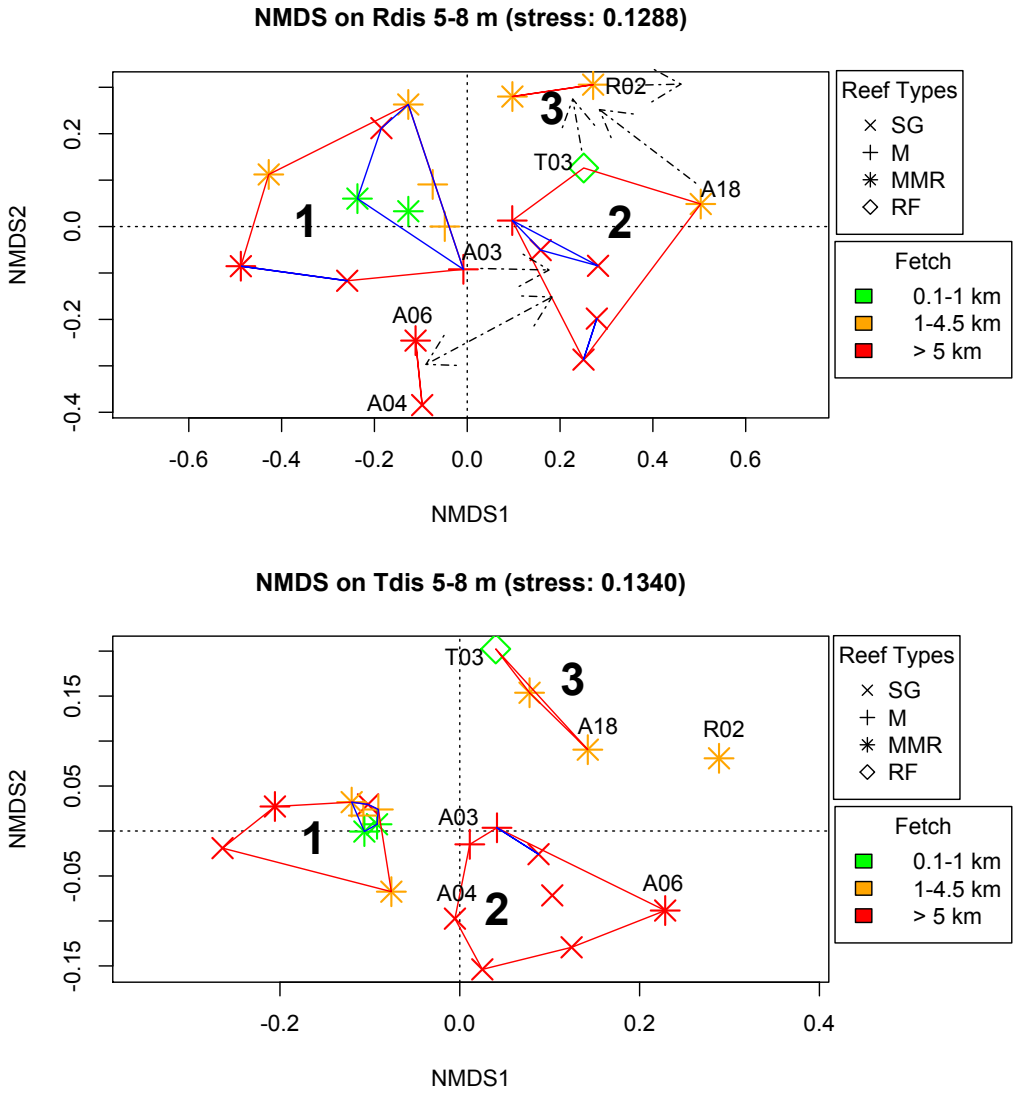


Figure 7.14 Comparison between an *Rdis*-based NMDS (top) and *Tdis*-based NMDS (bottom) for sites at five to eight metres depth. Reef types are indicated by symbols. The higher level clusters are shown in red and the lower level cluster are shown in blue. The cutting levels are the same as in Figure 7.5

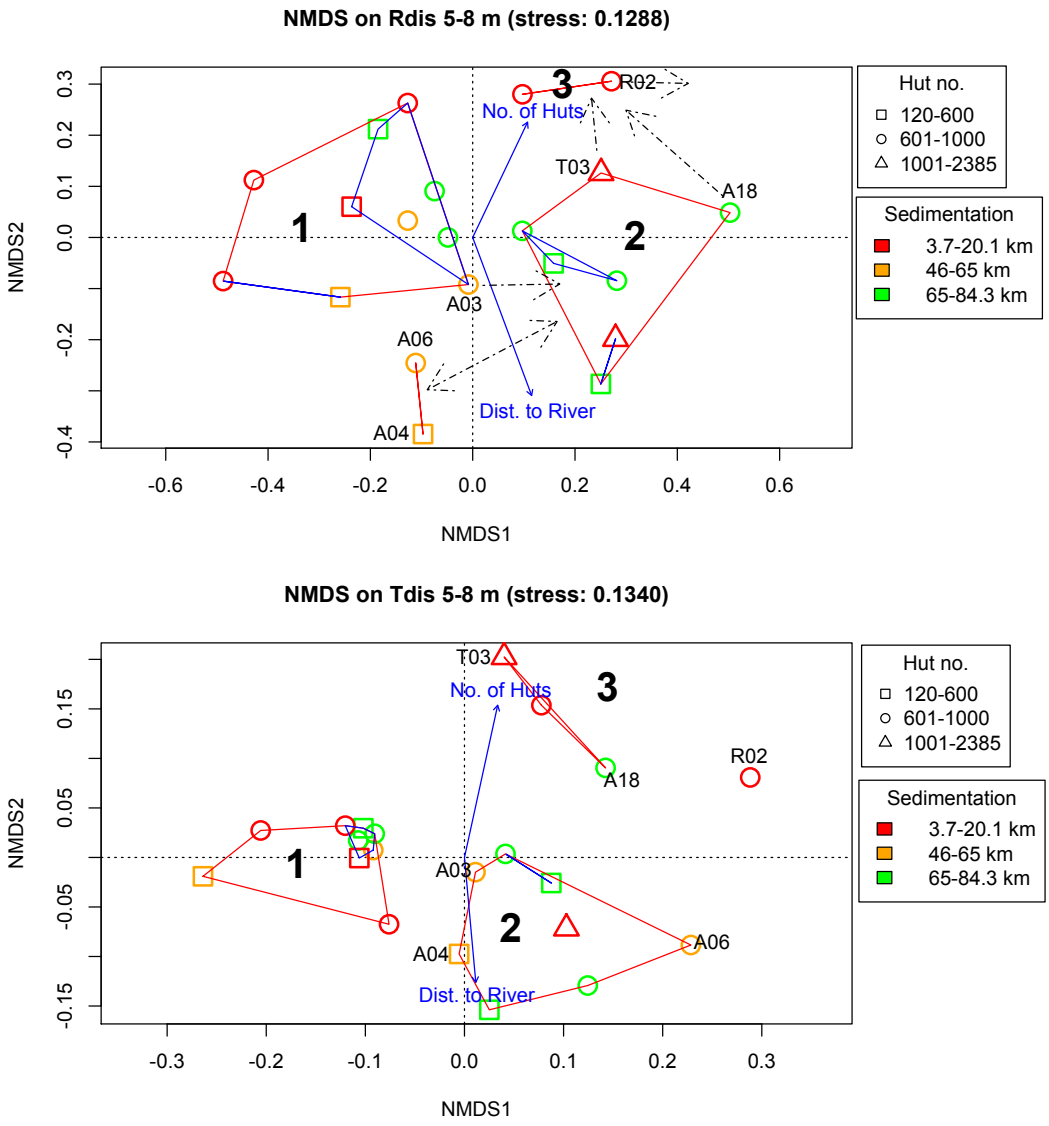


Figure 7.15 Comparison between an *Rdis*-based (top) NMDS and *Tdis*-based (bottom) NMDS for sites at five to eight metres depth. Environmental vectors (no. of huts and distance to nearest river mouth) for the ordination are show as blue arrows. The higher level clusters are shown in red and the lower level cluster are shown in blue. The cutting levels are the same as in Figure 7.5.

7.3.2.4. NMDS plots with Environmental variables at 8-15m

The only large-scale movement that occurred at this depth range was the movement of site A02 out of Cluster Two. Site A02 contained nearly 60 percent *Isopora* (45 percent *Acropora cuneata* and 15 percent *Acropora palifera*) while the rest of Cluster Two contained sites with quite diverse communities containing species from mostly non-*Acropora* emergent clusters. Cluster One contained mostly *Acropora*-dominated communities yet A02 was not placed in this cluster because of the distinct differences in trait combinations that exists between species in the emergent group *Isopora* and most other *Acropora* species (i.e. lack of axial polyp and brooding of larvae instead of spawning).

While there was no large-scale movement in or out of Cluster One there was much movement within this cluster. This is used as an example of how *Tdis* can cause small-scale reshuffling of sites and is discussed in detail in the next section. Species overlap for the sites in Cluster Two were high and therefore there is little change in this cluster as one moves from the *Rdis* to *Tdis*-based NMDS.

In terms of environmental variables Cluster Two consisted mainly of spur and groove sites which were (obviously) outside the barrier, the distance to river mouth for most sites was less than 20 km but it is doubtful that sedimentation had a big impact on these sites as the spur and groove formations suggest that the flushing effect here is quite strong. The population density of fishermen for sites in Cluster One was variable, however, because of the depth and locations outside the barrier these sites are more difficult to fish overall.

In terms of environmental variables Cluster One contained diverse reef types, fetch, distance to river mouth and population density. Note that when using *Tdis*, sites with similar environmental variable cluster far better on smaller scales than when using *Rdis* (this is discussed further in the next section).

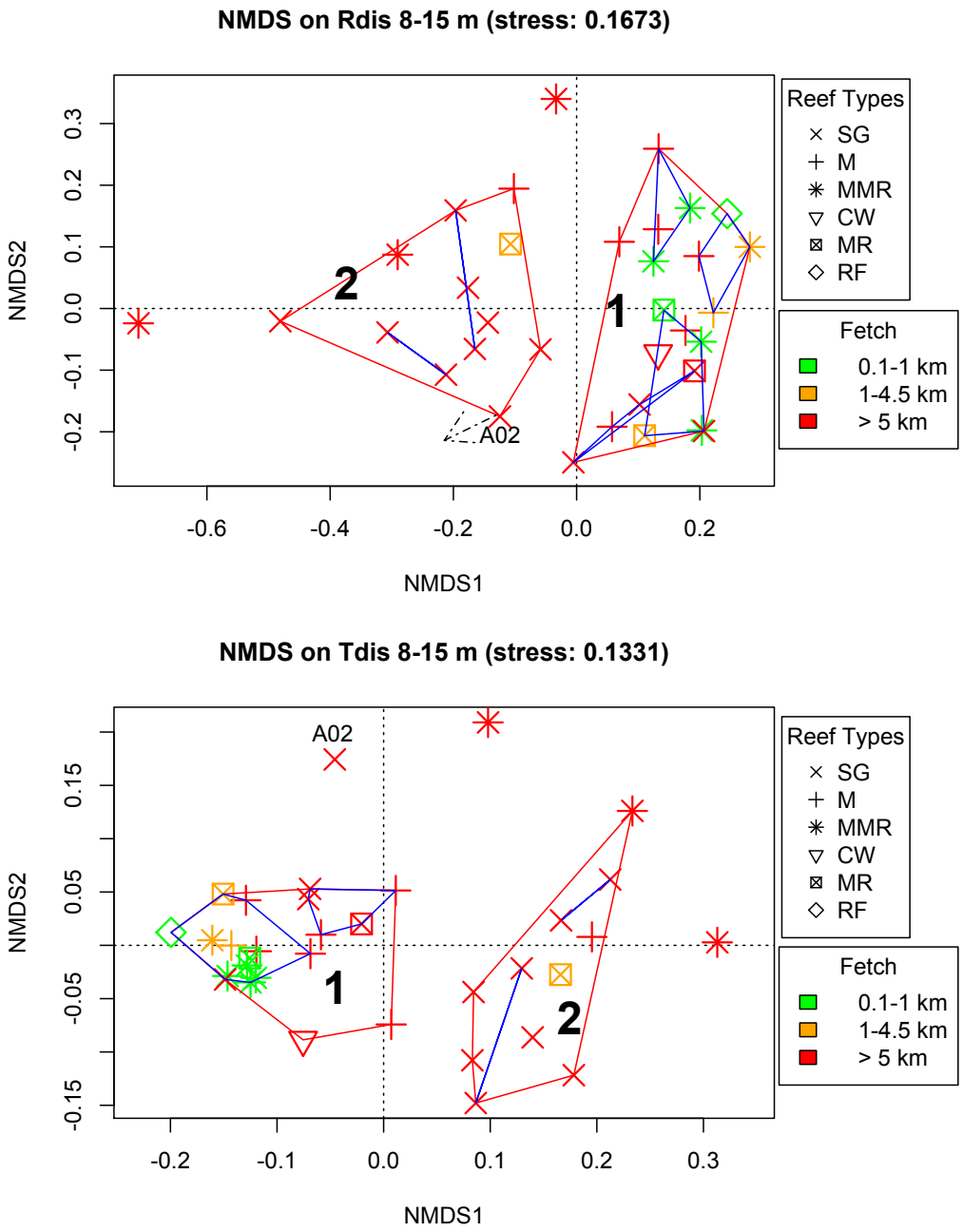


Figure 7.16 Comparison between a *Rdis*-based (top) NMDS and *Tdis*-based (bottom) NMDS for sites at eight to 15 metres depth. Reef types are indicated by symbols. The higher level clusters are shown in red and the lower level cluster are shown in blue. The cutting levels are the same as in Figure 7.7.

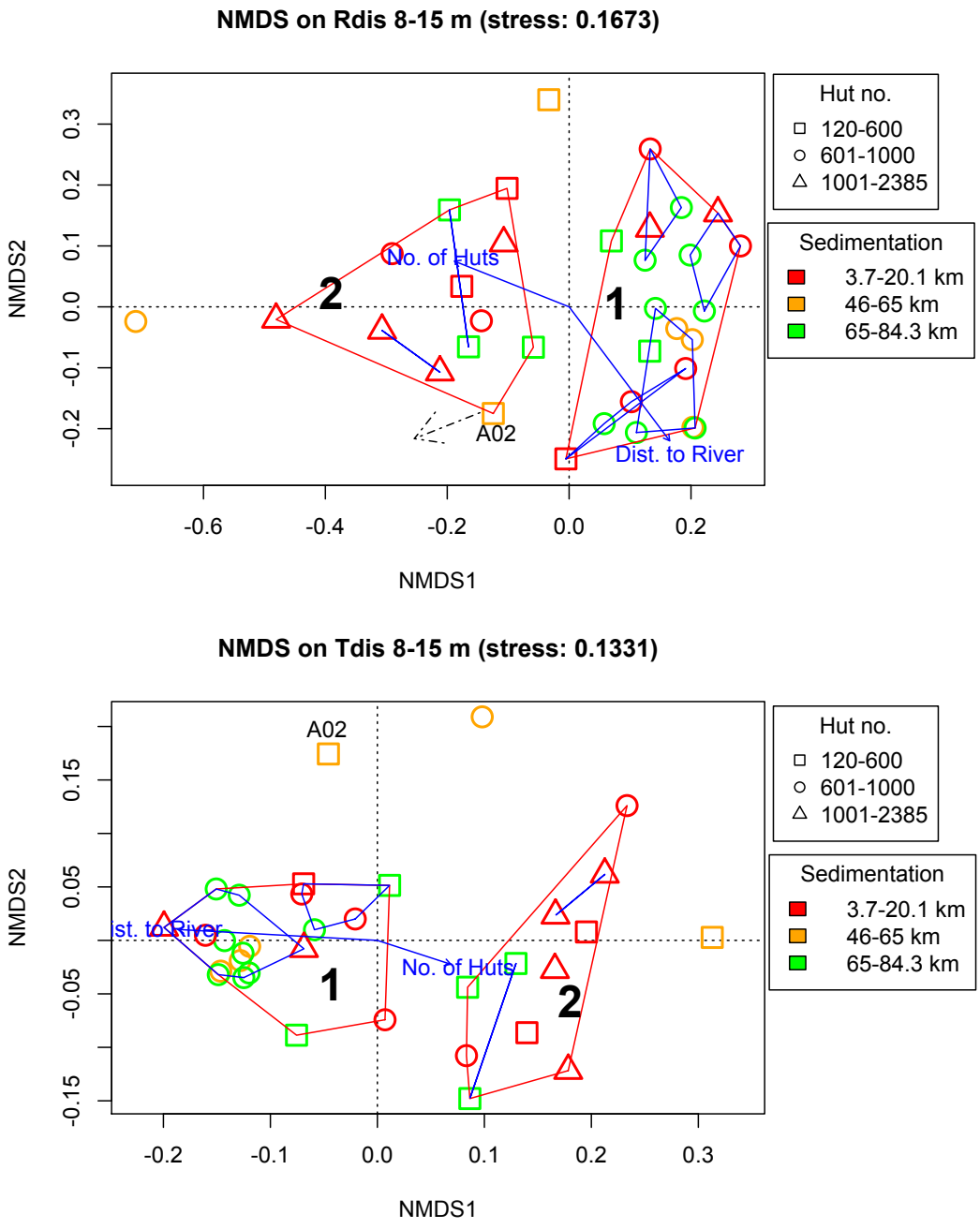


Figure 7.17 Comparison between a *Rdis*-based (top) NMDS and *Tdis*-based (bottom) NMDS for sites at eight to 15 metres depth. Environmental vectors (no. of huts and distance to nearest river mouth) for the ordination are show as blue arrows. The higher level clusters are shown in red and the lower level cluster are shown in blue. The cutting levels are the same as in Figure 7.7.

7.3.2.5. NMDS plots with Environmental variables at 15-26 m

The only large-scale movement for this depth zone that occurred when moving from *Rdis* to *Tdis*-based NMDS plots was that T02 moved from Cluster One to Cluster Two and of A09 moved out of Cluster One.

The *Tdis*-based NMDS plot identified A09 as an outlier while the *Rdis*-based NMSD plot included it Cluster One. Placement of A09 into Cluster One is awkward since it contains 28 percent *Isopora*, 36 percent *Diploastrea heliopora*, and 36 percent Laminar species while the remaining sites in Cluster One were dominated by *Acropora* spp. while a few sites contained small amounts of *Isopora* (which is why the *Rdis*-based NMDS placed A09 in this group). The *Tdis*-based NMDS moves A09 out of Cluster One because of *Diploastrea heliopora*'s unique trait set (it is the only coral in the region to have a mixed breeding system with both female and male polyps within the same colony) and also because of the large amount of *Isopora*. Whilst species in the emergent group *Isopora* (*Acropora cuneata* and *Acropora palifera*) are members of the genus *Acropora,* they are very different from other *Acropora* species in terms of traits.

T02 was placed in Cluster One in the *Rdis*-based NMDS due to the overlap it had in terms of *Astreopora myriophthalma* (33 percent) with R14 (37 percent), A29 (31 percent), and R13 (61 percent). However the remainder of R14, A29, and R13 was comprised mainly of *Acropora* species while the remainder for T02 contained 33 percent *Porites* massive species and 33 percent *Oulophyllia crispa*. This very different remainder composition caused T02 to be placed with A22 and A08 in the *Tdis*-based NMDS.

The environmental variables for sites within clusters at this depth range were quite variable, perhaps indicating that at this depth a certain amount of buffering against environmental variables is afforded.

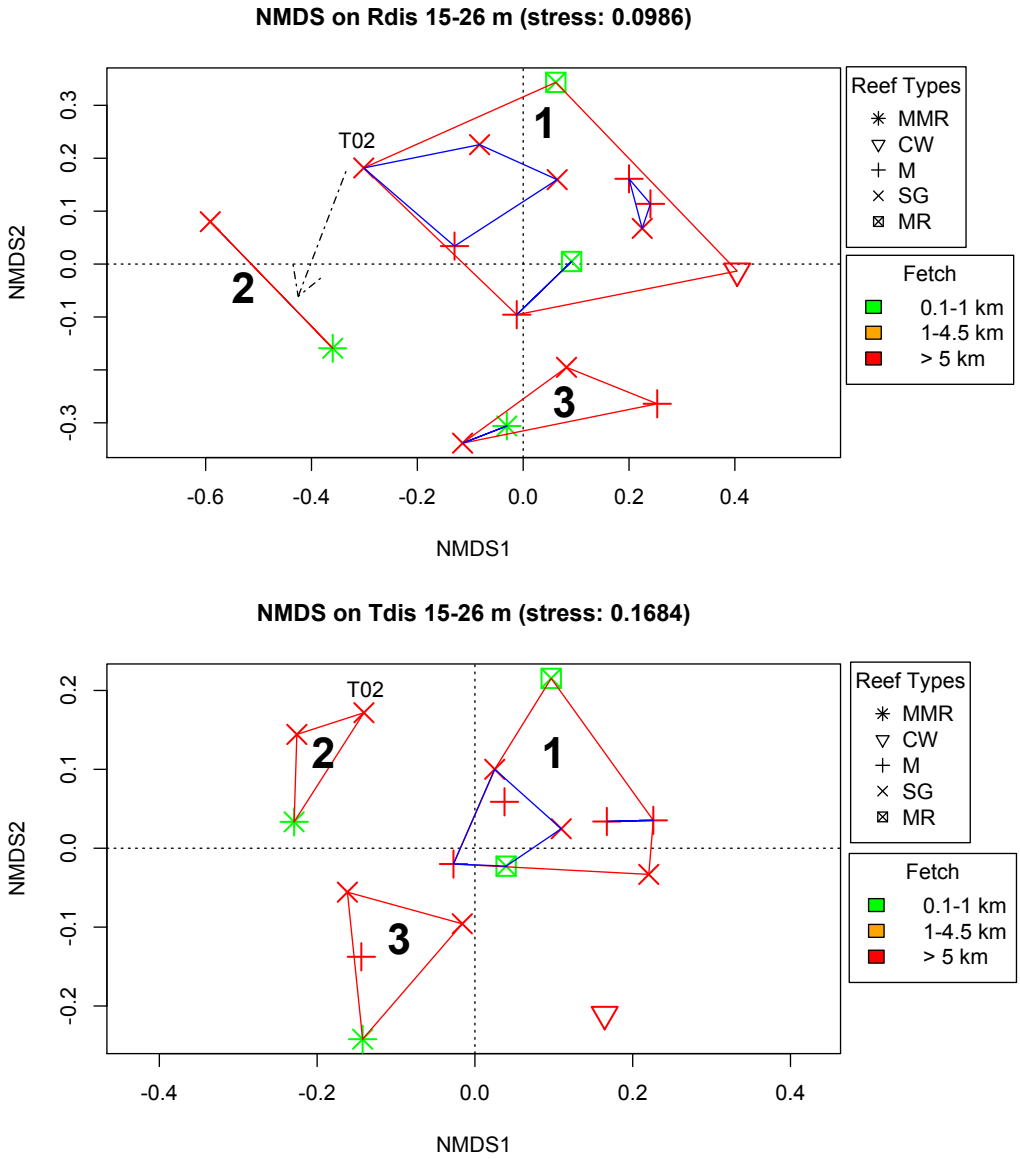


Figure 7.18 Comparison between an Rdis-based NMDS (top) and *Tdis*-based NMDS (bottom) for sites at 15 to 26 metres depth. Reef types are indicated by symbols. The higher level clusters are shown in red and the lower level cluster are shown in blue. The cutting levels are the same as in Figure 7.9

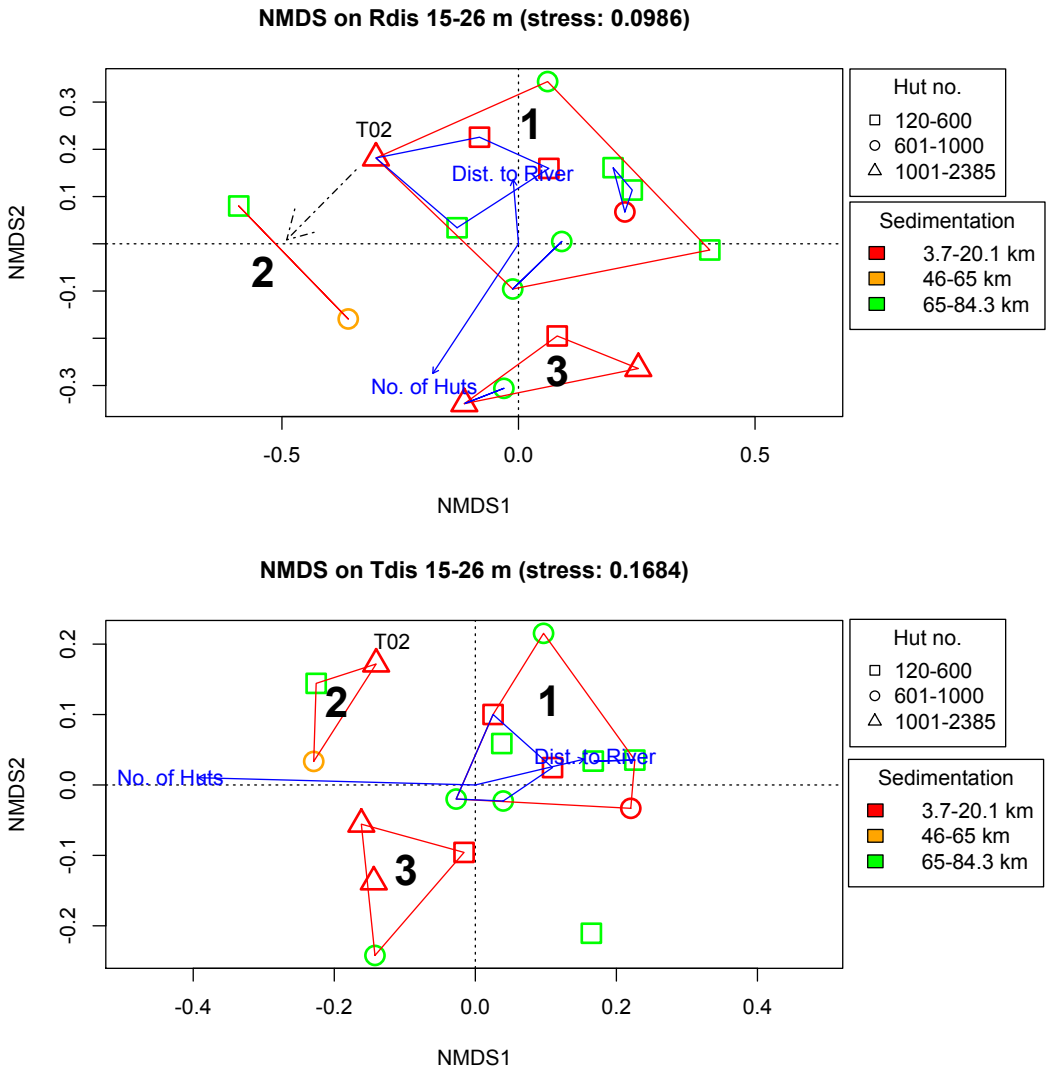


Figure 7.19 Comparison between an Rdis-based NMDS (top) and *Tdis*-based NMDS (bottom) for sites at 15 to 26 metres depth. Environmental vectors (no. of huts and distance to nearest river mouth) for the ordination are show as blue arrows. The higher level clusters are shown in red and the lower level cluster are shown in blue. The cutting levels are the same as in Figure 7.9.

7.3.3. Examples of smaller-scale ordination differences Tdis vs Rdis

Here I illustrate how *Rdis* and *Tdis* differ by examining Cluster One in the *Rdis* and *Tdis*-based NMDS for the eight to 15 metre depth zone. While this large scale cluster was the same for *Rdis* and *Tdis* the sites within this cluster were placed very differently within the cluster (see Figure 7.20).

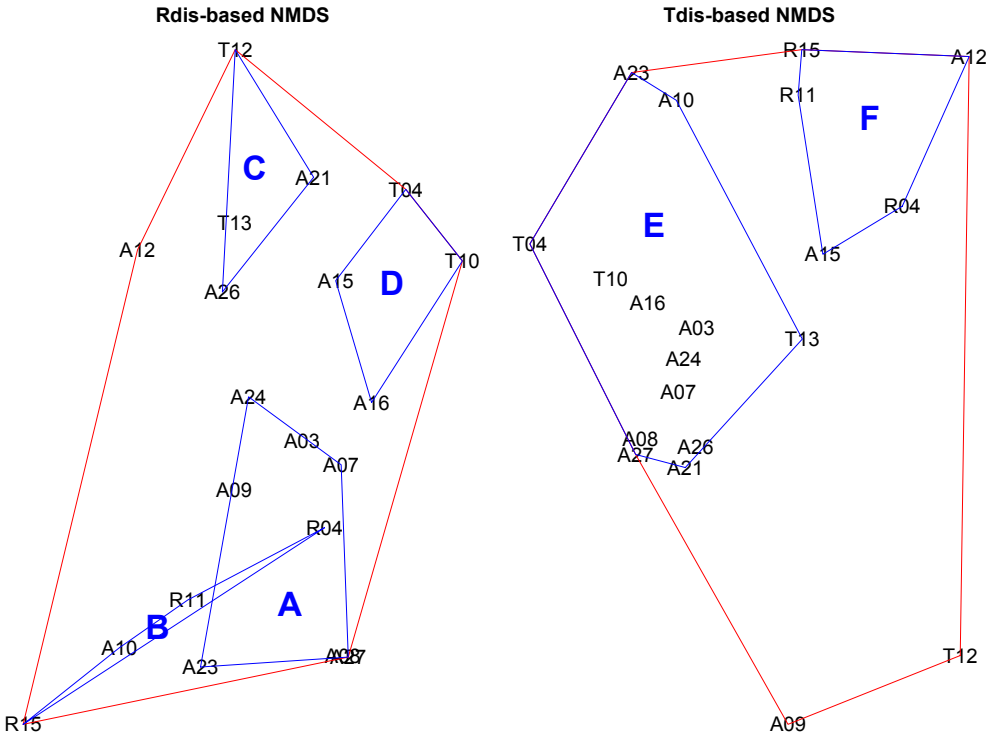


Figure 7.20 Cluster One from the *Rdis*-based NMDS (left) and *Tdis*-based NMDS (right). Note that while Cluster One (red contour; *Rdis* = 0.93, and *Tdis* = 0.35) for both NMDSs contain the same sites, the smaller level clustering structures (blue contours; *Rdis* of 0.7, *Tdis* of 0.25) contain very different sites and structures.

Furthermore the small-scale structures resulting from the *Tdis*-based NMDS (Cluster E and F in Figure 7.20) were more ecologically sensible than those resulting from the *Rdis*-based clusters (A-D in Figure 7.20). The more logical structure of the *Tdis*-based NMDS clusters can be seen by comparing bar plots of species composition for all sites in Cluster One with the small-scale clusters (A-F) overlaid (see Figure 7.21 and Figure 7.22).

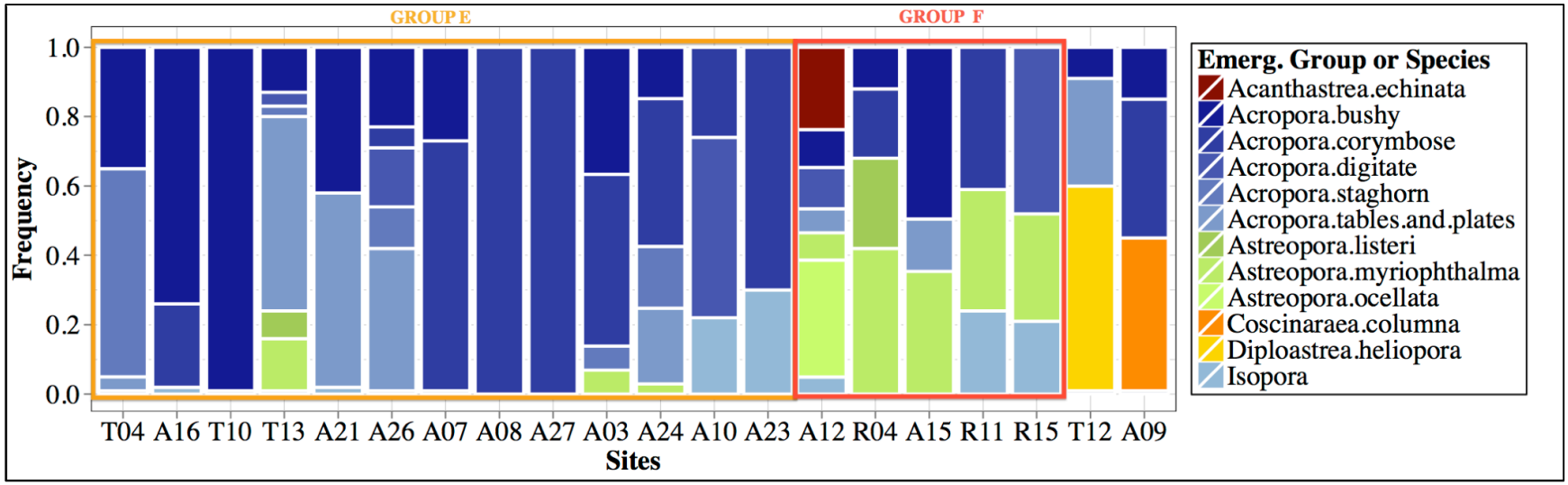


Figure 7.21 Clusters of sites deemed similar based on *Tdis*-based NMDS with groups resulting from the cluster analysis overlaid. The NMDS showed two clear clusters: group E, which is largely based on trait similarity between *Acropora* species, and group F, which is based on trait similarity between *Acropora* spp., *Acanthastrea* spp. and *Astreopora* spp. The *Tdis*-based NMDS identified T12 and A09 as outliers within Cluster One.

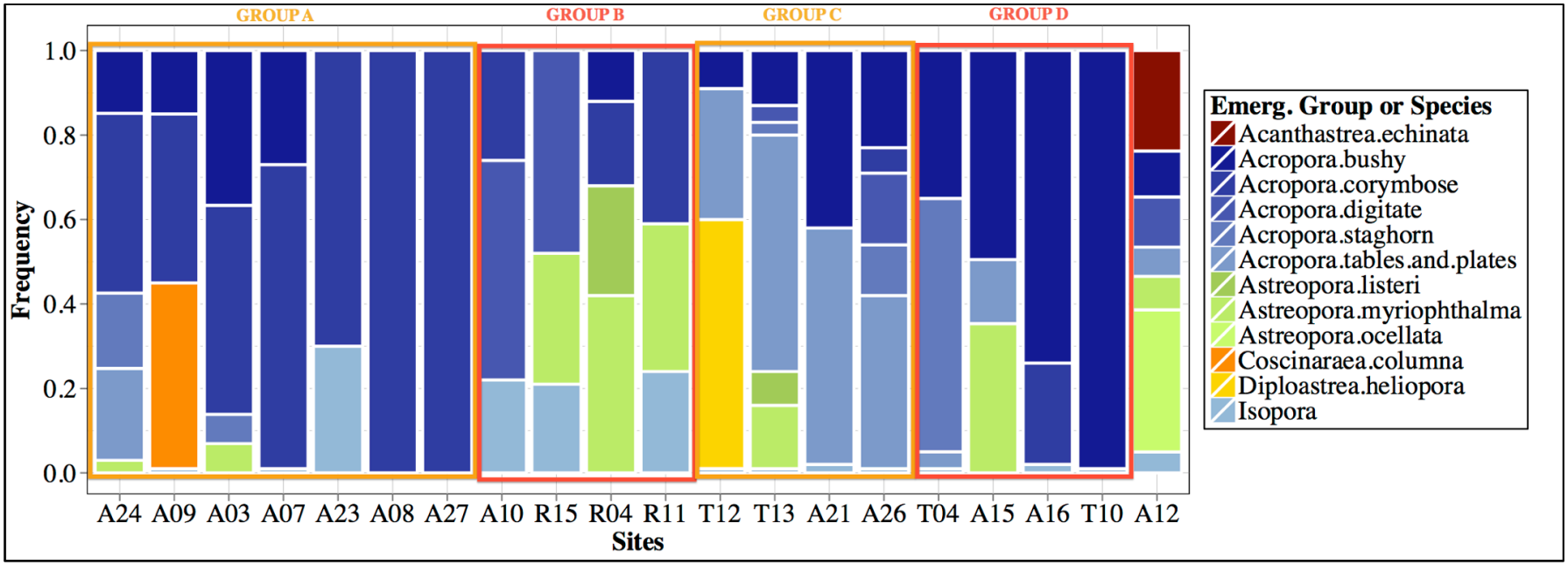


Figure 7.22 Clusters of sites deemed similar based on *Rdis*-based NMDS with groups resulting from cluster analysis overlaid. The NMDS showed four clear clusters groups A-D and one outlier A12. Note the awkward placement of A10, A09, T12, and A15 in terms of emergent group and species composition as compared to the more sensible placement of these sites in the *Tdis*-based groups shown in Figure 7.21

In the *Tdis* based barplot, all *Acropora* dominated sites are grouped together in Cluster E (Figure 7.21) while all sites dominated by *Astreopora* spp., *Acanthastrea echinata*, *Acropora* spp., and I*sopora* were place into Cluster F. Both T12 and A09 were identified as outlier within Cluster One despite having *Acropora* species present due to their very different remainders (*Diploastrea heliopora* in T12 and *Coscinarea columna* in A09).

In contrast, the groupings based only on overlapping species (Figure 7.22) resulted in some rather awkward placements (see for example A09 in Group A, A10 in Group B, T12 and T13 in Group C, and A15 in Group D). Also the identification of A12 as being an outlier in Cluster One is inappropriate considering the high level of trait combination overlap it has with the sites in Group F (see Figure 7.21).

7.4. Conclusion

7.4.1. Is Tdis better than Rdis?

For each site pair the following scenarios are possible in regards to *Rdis* and *Tdis*:

1. Both *Rdis* and *Tdis* are high; sites are placed close to each other in both *Rdis*-based and *Tdis*-based ordinations.
2. Both *Rdis* and *Tdis* are low; sites are placed far apart in both *Rdis*-based and *Tdis*-based ordinations.
3. *Rdis* is low, but *Tdis* is high; sites are placed far apart in the *Rdis*-based ordination but close together in the *Tdis*-based ordination.
4. *Rdis* is low, but *Tdis* is high; sites are placed close together in both the *Rdis*-based and *Tdis* based ordination.

This last scenario seems counter intuitive but occurs when sites are positioned closely due to their relationships to other sites within the cluster, in other words, they get ‘pushed’ into the ‘right’ position by default.

So then, *Tdis* is ‘safer’ to use than *Rdis* because one does not risk scenario 2 above i.e. the placement of two functionally similar sites far apart in an ordination. Also it provides a ‘fine-tuning’ of position, which results in overall tighter clustering and

lower levels of dissimilarity between sites in a cluster (this was shown in Figure 7.3 to Figure 7.9). Also *Tdis* avoids the difficulties imposed by having many site pairs that are considered completely dissimilar (as can be seen by comparing the Shepard diagrams between the two methods in Figure 7.1) which results in an overall better goodness of fit of sites in the ordination (Figure 7.2).

I think the major disadvantage with *Tdis* is also ironically one of its greatest advantages: the user defines what traits are important in terms of defining similarity. On one hand it is very useful to be able to select a number of traits and then weight them in a particular manner especially if one is interested in a particular reef feature such as bleaching sensitivity. For example, through experimentation one might determine that *Symbiodinium* clade associations, the ability to reshuffle *Symbiodinium* clades under stress, colony morphology, and tissue thickness are the most important traits for determining bleaching sensitivity. Also through experimentation one could determine the relative importance of each trait and allow this to determine their weighting in the calculation of *Tsim*. This is a major advantage as it provides the researcher a similarity metric for specific reef functions of sites in, say, an MPA.

On the other hand, if the user selects traits that are not truly related to the function of interest, or weights them in very inappropriate manner, then the resulting ordinations may be misleading.

In this study I used 26 life history traits spanning a total of 136 attributes and did not focus on a particular 'function' and therefore weighted all of the traits equally. Of these 26 traits, six were related to colony morphology (colonality, colony morphology, minimum surface index, maximum surface index, morphological plasticity, and reef attachment) so there is a chance that colony morphology may have been slightly over-weighted in the calculation of *Tsim*, then again, colony morphology is a very important feature (and hence one arrives back to the difficulty of deciding how to weight traits).

Finally, it is my opinion that *Tdis* is more useful than *Rdis* because it allows the user to account for the redundancy of species in terms of *particular* traits combinations

(i.e. species that can replace one another in an ecosystem as interchangeable parts). I think great care must be taken in stating that species are redundant only for the particular traits under consideration since individual species may have important traits not yet discovered or measured. Consequently one should not use measures of redundancy as a justification to only protect one of the species in a 'redundancy group'.

8.
General discussion and conclusion

"We can say something about the community by giving a list of its species composition, but a community is poorly described by such a list alone."

(Whittaker, 1975)

"When an ecologist says 'there goes the badger,' he should include in his thoughts some definite idea of the animal's place in the community to which it belongs, just as if he had said, 'there goes the vicar'."

(Sutherland, 1927).

8.1. Introduction

For nearly a century, ecologists have formally recognized that it is not enough to merely inventory the species present in an ecosystem; one must also consider what the species 'do' within it. Spurred on by increasing environmental changes, research into what species 'do' has gained momentum in past decades. More specifically, focus has largely shifted from species-level data to trait-level data. This shift in focus is so fundamentally different that some have called it a renaissance (McGill et al., 2006).

If we ignore intra-specific trait variation, which we must since such level of trait detail is not generally available for coral species, we can draw the analogy of the traits that a species possesses as being like a hand of cards it is dealt. The cards (traits) that a species 'holds' are played in different combinations against its surrounding environment. Ultimately species with a favourable hand will 'win' (persist) while others with less favourable cards will 'lose' (perish). Whilst the observation that particular trait-combinations favour survival in particular environments may be fairly obvious, we know surprisingly little about the dynamics of how trait combinations operate on scales relevant to community ecologists.

The 21st century will continue to present increased extremes of environmental conditions including increases in: water temperatures, storm frequency, algal-coral competition (due to overfishing of herbivores) and terrigenous sediments on reefs

(due to inland deforestation). It is vital that research resources are shifted towards understanding how Scleratinian trait-combinations relate to these environmental extremes in the community context.

Whilst plant ecologists have made substantial progress in trait-based community ecology research, reef ecologist have understandably lagged behind as corals are far more difficult to access, slower growing, and are also more difficult to manipulate in laboratory experiments. Further, coral reef research rarely enjoys the level of research funding of the large-scale agricultural industry in the developed world. Despite these challenges an impressive body of *Scleractinian* trait-level data has accumulated.

One underlying aim of this project was to examine both the depth and breadth of what *Scleractinian* trait data is available and what is known about how these traits relate to the persistence of particular species in specific environments. Overall, it was found that a wealth of morphological, physiological, and behavioural traits are available in the literature, but because these resources are scattered many researchers will not have the time or resources to compile the trait data needed to undertake trait-based reef ecology research for the corals in their particular biogeograpical region of interest.

As discussed earlier, the data bottleneck described above can be alleviated by compiling coral trait data into an online database. The task of compiling all the traits for all the corals in the world and making them available online is outside the scope of any PhD project, and indeed any one person. Rather what is needed is an open source online database platform that allows the coral reef research community at large to create, edit, and verify content.

Another fundamental motivation for this PhD project was to adapt the statistical tools that community ecologist tend to use most commonly (multi-variate statistical tools) so that they can handle trait-data. This is a critical step since it provides a familiar (but adapted) methodological toolkit, which will not require a steep learning curve for use and implementation. The advantages of the Trait similarity metric (*Tsim*)

have been discussed in the conclusions of previous chapters and will therefore not be mentioned further here.

Here I summarise the overall outcomes and findings of this project.

8.2. Overview of outcomes

This dissertation examines key steps in both the development and implementation of trait-based approaches in reef ecology. The specific outcomes and tools developed during this dissertation are:

1. Following a review of approaches to date (Chapter One) and examination of suitable trait data (Chapter Two), a life history trait database containing 26 life-history traits spanning 136 attributes for species in Southwest Madagascar was created (see Digital Supplement 1.1.3).
2. An inventory of the locations and reef types for 66 reefs in Southwest Madagascar, an under-studied region of the world where reef locations are poorly mapped in many cases (Chapter Three).
3. A replacement methodology based on species commonality so that species difficult to distinguish from one another, such as certain species of *Acropora* and *Montipora*, can be included in trait-based analysis as specific species (Chapter Four).
4. Identification of 13 *Scleractinian* emergent groups based on traits, that is, species with highly similar trait sets that can be considered functionally redundant for these trait sets (Chapter Five).
5. A novel trait similarity measure, *Tsim*, which allows the user to determine how similar reefs are in terms of particular trait-combinations (Chapter Six).
6. A package of R functions (see Digital Supplement 1.3) that allows the user not only to calculate *Tsim* but visualize *Tsim* scores between two reef sites using several graphical tools such as abundance weighted heat maps (AWH; Chapter Six) and emergent group plots (Eplots; Chapter Six).

7. A clear demonstration, using real data, that trait-based similarity measures such as *Tsim* have clear advantages over conventional species-based similarity measures (Chapter Seven).

8.3. Summary of findings

Overview of major findings:

1. Trait-based approaches in reef ecology have been under-explored and many of the tools developed initially for plant ecology are easily transferrable to corals due to their non-mobile nature and dependency on light.
2. While many traits are available for use in reef ecology some are difficult to use in trait-based ecology because of their environmental plasticity (for example growth rate) therefore when recording coral trait data it is especially important to record the environmental conditions under which the trait was observed (i.e. depth, flow regime).
3. While clear emergent groups exist for most corals in Southwest Madagascar about 25 percent have trait combinations unique enough that placement into emergent groups is inappropriate and therefore emergent group approaches should not be used alone in trait-based analyses.
4. Trait-based similarity metrics are safer to use than species-based similarity metrics because they do not risk missing site pairs that are functionally similar despite being mechanically dissimilar.
5. For reefs in Southwest Madagascar trait-based similarity metrics produce ordinations with lower stress, tighter placements of sites in clusters, clusters with higher levels of similarity and clusters with high self-similarity in terms of environmental variables

8.4. Strengths and weaknesses of a trait-based research approach to coral reef ecology

Perhaps the most important strength of a trait-based approach, at least in terms of trait-based similarity measures, is that sites that are functionally similar but mechanically different are not ignored. Further, use of trait-based similarity measures avoids the ‘absolutist’ approach taken by species-based similarity measures i.e.

considering individuals within a species to be either completely similar and individuals from different species to be completely different.

As mentioned in Chapter Seven, one of the key strengths with trait-based approaches can also become a weakness: the user selects traits of interest and their weighting scheme. On the one hand, this creates a new avenue for comparing reefs in terms of functions and resilience or resistance to specific environmental stressors. It may also be a useful tool for exploring the dynamics of the ecological phase-shifts that have been observed to occur with increasing frequency between coral-dominated and non-coral dominated reefs. On the other hand, if the relationships between traits and functionality and/or resilience are poorly understood or particular traits are incorrectly weighted then the results may be misleading.

Another advantage of using trait-based metrics is that they take into account that some coral species are very similar while others are not. Of course, one may argue that simply moving the level of measurement up the taxonomic tree will produce similar results, however, this is inappropriate for the following reasons. While it is true that more closely related species are more likely to have similar trait sets, there is plenty of evidence of convergent evolution occurring within the order *Scleractinia*. Also, since genetics entered the toolbox driving major taxonomic revisions within the order *Scleractinia* (Fukami et al., 2008), earlier taxonomic relationships should not be overly relied upon. In addition, even within a genus, traits may be so variable between species that surveys conducted at the genus or family level cannot be expected to capture the essential information in the way that functional groups might. Ultimately, there is no avoiding the point that the useful unit of measurement for many ecological applications must be at the trait-level.

This brings us to back to a key disadvantage of trait-based research: the initial gathering of trait data for coral species can be labour intensive. However, this dissertation provides some basic tools and findings that will substantially lessen the effort required for future research. For example, the overlap in biogeographical distributions between coral species in Southwest Madagascar and the Chagos Archepeago is high, thus, transferring the methodologies presented in this

dissertation to this important MPA (Sheppard et al., 2012) would require little additional trait-data collection.

8.5. Future directions

Since this dissertation represents, to my knowledge, the first attempt at using a trait-based similarity metric as the basis for comparing community similarity on reefs (or indeed any other ecosystem) the scope for future work is immense. What follows is what I believe to be the most important short-term steps towards establishing trait-based approaches as commonplace in coral reef community ecology:

1. Creating an open-source online community run database platform where reef ecologists (and potentially aquarist) can upload, edit, and discuss coral trait data.
2. Encouraging collaborations between those currently conducting trait-based research in plant ecology and those with interest in doing so within reef ecology
3. Continue the essential research into the basic autecology of coral species
4. Promote the use 'R' among reef ecologists since most tools currently available for trait-based ecology exists within this platform.

The first two tasks are presently being done at Warwick.

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Appendices

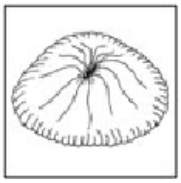
1. Detailed morphometric traits

Morphometric traits are those, which involve measuring the external shape and dimensions of corals. Such traits are observable either directly or under a microscope. The morphological data used in this study was taken from the taxonomic reference Coral ID (Veron, 2000). The morphometric traits available in Coral ID can be divided into three categories depending on the scale and location of measurement: colony, corallite, and inter-corallite level morphometric traits.

Following is a summary of the trait descriptions as laid out by Veron (2000).

1.1. Colony-level morphometric traits

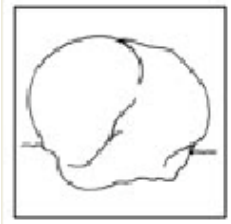
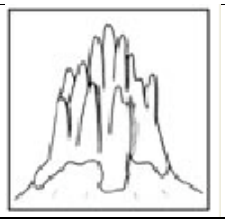
1.1.1. Colonality

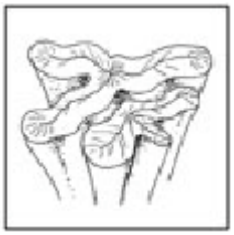
	State	Description
	multiple mouths or corallites	The coral colony consists of multiple mouths or corallites
	one mouth or corallite	The coral consists of only one corallite and has only one mouth

1.1.2. Attachment to reef

	State	Description
	attached	Corals attach to the substrate. This applies to most coral species.
	free-living	Corals that are not attached to the substrate.

1.1.3. Colony growth-form

	State	Description
	branching	Colonies that are primarily composed of branches of any sort. This is a common growth-form inclusive of a very wide range of shapes
	hemispherical or submassive	Colonies which are broadly similar in all dimensions (have a small surface area to volume ratio) and are mostly solid beneath the surface. This is a common growth-form inclusive of a wide range of shapes.
	encrusting	Colonies that are thin and adhere to the substrate so that their shape is dominated by the shape of the substrate. A common growth-form that may occur with others. Most colonies are initially encrusting
	solid plates	Colonies that are primarily two-dimensional and solid. They may be partly or wholly attached to the substrate, but are not encrusting and do not closely follow the contours of the substrate. A growth-form that may occur with others.
	perforated plates and tables	Colonies that are primarily two-dimensional and are formed of fused branchlets which do not form a solid plate. This morphology is found mostly in *Acropora*.
	columnar or digitate	Colonies which form columns as the dominant morphology. A growth-form mostly found in large colonies.

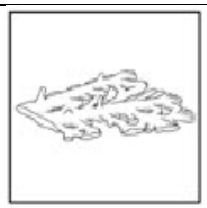
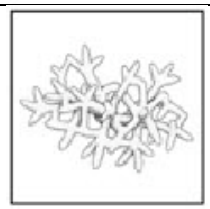
	State	Description
	foliose	Colonies which have leaf-like fronds or which consist of thin sheets (less than three mm thick) which are not encrusting. Many delicate colonies have this growth-form.
	disc like	Colonies and individuals which have determinate growth-forms resembling discs. These are mostly solitary free-living fungiids.
	flabello meandroid	Colonies with valleys that have completely separate walls. Valleys have several mouths. An uncommon growth form where the colony shape is determined by the presence of flabello-meandroid valleys.
	phaceloid	Colonies composed of tubular corallites which have completely separate walls. An uncommon growth form where the colony shape is determined by the presence of elongate corallites joined only at their base.

1.1.4. Branching

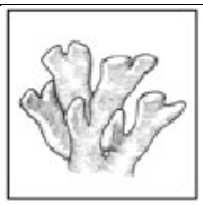
1.1.4.1. Branching dominance

	State	Description
	2D dominant	Branching colonies which have a predominantly two-dimensional growth form. Mainly *Acropora* take on this morphology.
	3D dominant	Branching colonies which have a predominantly three-dimensional growth form. Most branching corals take on this shape.
	absent	Colonies have no branching at all

1.1.4.2. Branch fusion

	State	Description
	2D	Branching colonies where the branch tips fuse with other branch tips in predominantly one plane to form a two-dimensional structure.
	3D	Branching colonies where the branch tips fuse with other branch tips in all directions to form a three dimensional stucture
	none	Branching colonies where the branch tips are free and do not fuse with other branch tips.

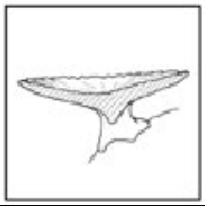
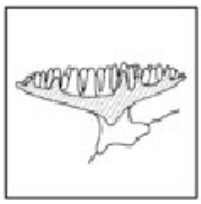
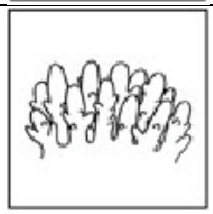
1.1.4.3. Branch ends

	State	Description
	flattened	Branching colonies where the branch tips are flattened.
	not flattened	Branching colonies where the branch tips are not flattened. Most branching corals take on this form.

1.1.4.4. Distinct primary branches

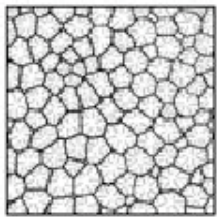
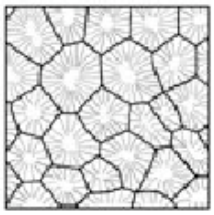
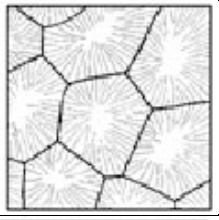
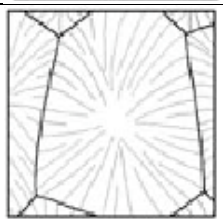
	State	Description
	axial	Colonies have strongly conscipuously primary branches, which are axial. Branches can be traced from the centre of the colony to the tip of the branch and are generally linear. Mainly *Acropora*.
	inconspicuous or absent	Distinct primary branches are absent. All branches are of similar size or form or, if branches are different from one another, a central main largely linear branch cannot be distinguished.
	not axial	Primary branches are present but few if any can be traced from the colony centre to a single branch tip and they may not be linear. However, branching is not predomiantly haphazard.

1.1.4.5. Sub branches

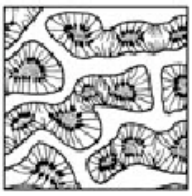
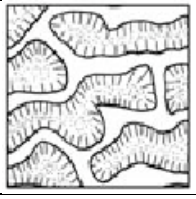
	State	Description
	2D	Sub-branches arising from main or central branches are only found in a two dimensional plane and normally join one primary branch to another forming a perforated table. This state occurs mainly in *Acropora*.
	2D plus	This state only ocurs in *Acropora* where the colonies form tables with vertical branchlets. These are corymbose colonies where sub-branches aris from main or axial branches are found in a two-dimensional plane but additional branchlets project upwards,
	3D bottlebrush	This state describes a distinct growth form of *Acropora* called hispidose. Colonies have primary branches with sub-branches arising radially. The sub-branches form the secondary branches from which further sub-branches may arise radially. Corallites on primary branches tend to be short or immersed, while those on sub-branches become increasingly exsert.
	3D bush	Colonies have main branches with sub-branches arising radially. Further sub-branches may or may not arise radially or irregularly from the secondary branching.
	3D not conspicuous	Although there are sub-branches, the main branches totally dominate the colony, which appears digitate. Sub-branches tend to be near the base of the colony and can point in any direction from the central branch, although this is rarely neatly radial.

1.2. Corallite-level morphometric traits

1.2.1. Calice or valley width

	State	Description
	<1 mm	The corallite callice diameter or valley width is smaller than one mm
	1-5 mm	The corallite callice diameter or valley width is between one and five mm
	5-10 mm	The corallite callice diameter or valley width is between five and 10 mm
	>15 mm	The corallite callice diameter or valley width is greater than 15 mm

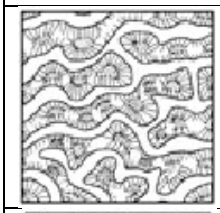
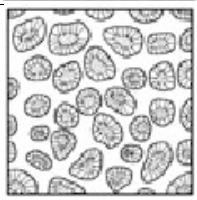
1.2.2. Corallite definition

	State	Description
	corallite centres distinct	Corallite centres are distinguishable
	corallite centres indistiguishable	Corallite centres are not distinguishable. This is uncommon but occurs ocassionally in meandering taxa.

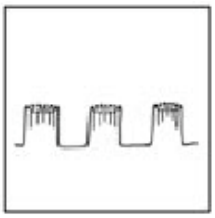
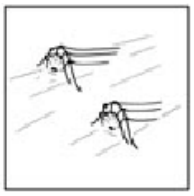
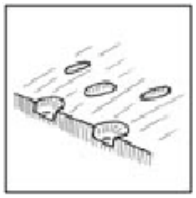
1.2.3. Corallite differentiation

	State	Description
	axial corallite present	Axial corallite are single corallites which occur on the tip of a branch and which are differentiated in size or form from other corallites. Mostly *Acropora*.
	central corallite present	Colonies in which the original (first) corallite is recognisable. This traits state is seldomly found in all colonies of a species
	neither axial nor central	Colonies which do not have distinguishable axial or central corallites. Most corals.

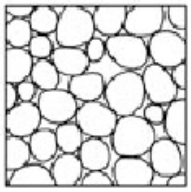
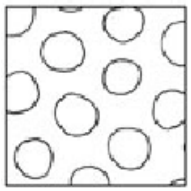
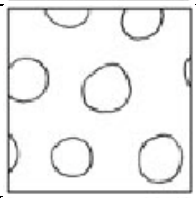
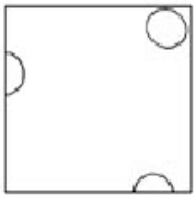
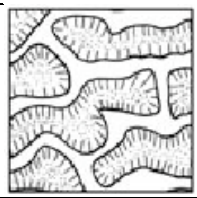
1.2.4. Corallite isolation

	State	Description
	corallites continuous	Colonies are formed of valleys or are dominanted by linked groups of two or more corallites. Valleys may have common walls (meandroid colonies) or individual walls (flabello-meandroid colonies).
	corallites seperate individuals	Colonies have individual corallites which are generally defined by a single mouth.

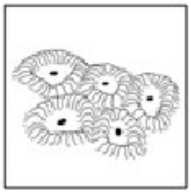
1.2.5. Corallite or valley protrusion

	State	Description
	exsert elongate or multicentric	Corallites are multicentric or elongate with indistinct centres and the resulting short or long valleys have walls that project above either skeletal matrix, ambulacral groove or space which separates them from the walls of adjacent valleys.
	exsert monocentric	Colonies whose corallites extend outwards between one quarter and twice their basal corallite diameter
	half immersed	Colonies where part of the wall of a majority of corallites is immersed in the coenosteum
	immersed	Corallites are embedded in skeletal matrix and corallite walls do not project above the general corallum. The skeletal matrix, coenosteum or extra-thecal region is visible between corallites. Corallites are irregularly spaced and do not join together in rows. *Montipora* has this trait state.
	recessed	Corallites are recessed into the corallum with adjoined walls. The skeletal matrix is not visible between corallites
	slightly exsert monocentric	Colonies whose corallites extend outwards less than one quarter of their basal corallite diameter
	strongly exsert monocentric	Colonies whose corallites extend outwards from the corallum more than twice their basal corallite diameter. Includes most colonies with tubular corallites

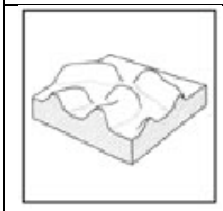
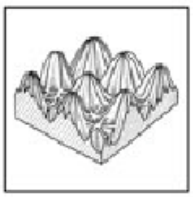
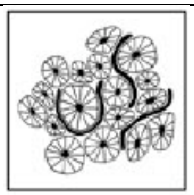
1.2.6. Corallite spacing

	State	Description
	crowded	Colonies where the majority of corallites are within one quarter of the width of the top of the corallite (outside wall to ouside wall) to other corallites in all directions, the measurement between corallites to be made from the outer edge of the wall at the base of the corallite
	fairly crowded	Colonies where almost all corallites are more than one quarter but less than one times the basal width of the corallite. Wider gaps are rare.
	well spaced	Colonies where the largest common gap between the bases of adjacent corallites is more than one but less than two times the basal width of the corallite.
	widely spaced	The widest common gap between corallites is two or more corallite diametres.
	indistinct	Colonies where corallite centres cannot be distinguished and where, therefore, spacing cannot be established. This is an uncommon trait state.

1.2.7. Corallite wall separation

	State	Description
	corallite walls separate	Corallites which have one or more mouths but which have a wall which is not shared except as a sideways continuation with other corallites.
	corallite walls adjoined	Corallites which have one or more mouths but which hae a common wall.

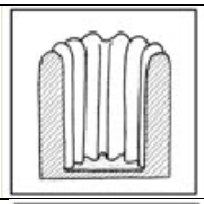
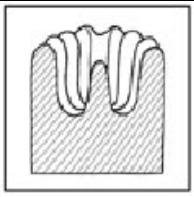
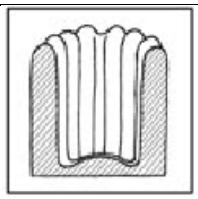
1.2.8. Corallite wall features

	State	Description
	dissected walls dominant	Valleys intersect each-other frequently but rather than forming monticules, walls are dissected into short lengths which are disconnected at one or both ends. A rare state but conspicuous when present. It occurs principally in *Hydnophora* and *Mycetophyllia*, but occasionally in other taxa such as *Colpophyllia* and *Symphyllia*.
	forms monticules	Valleys intersect each-other so frequently that walls are reduced to conical mounds. Typical of most colonies of *Hydnophora*, but this state is found in a few other taxa. Note this state varies within species according to environmental conditions.
	groove and tubercle structures	Fine tubular structures between corallites made of epitheca which are sometimes found in *mussids* and *faviids*.

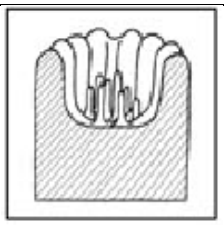
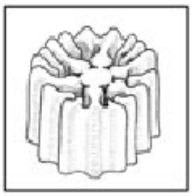
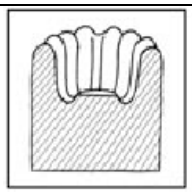
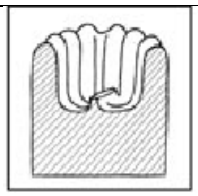
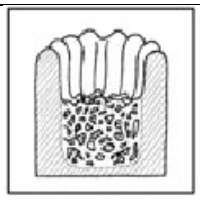
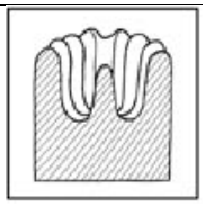
1.2.9. Columellae morphology

The columella is the central axial structure within a corallite, which is the skeleton of an individual polyp. Three columellae traits and their respective states could potentially be used in trait-based studies.

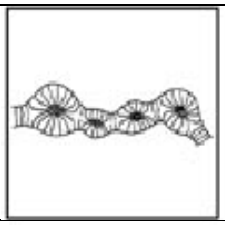
1.2.9.1. Collumella presence

	State	**Description**
	absent	The columella is absent
	conspicuous	Columellae are present and are conspicuous components of the corallite
	inconspicuous	Columellae are present but are inconspicuous components of the corallite

1.2.9.2. Columella form

	State	Description
	a group of spinules	Columella is formed by a group of vertically straight, not contorted or intertwined spinules
	forms deltas	A spongy columella is divided into 6 sections which look like paliform lobes. This occurs only in the genus Goniopora
	horizontally flattened	Columellae are solid and occur above the corallite floor but are horizontally flattened
	laterally flattened	Columellae are eith single laterally flattened structures or they form continuous walls
	septa like	Columellae are composed of one or more septa whose inner margins are aligned along the long axis of a valley
	spongy	Columellae appear spongy but do not lack rigity. This is a very common state
	style or club like	Columellae consist of a single vertical style or club shaped projections from the centre of the corallite.

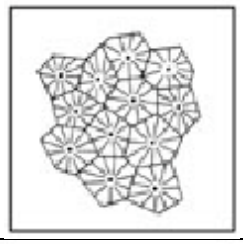
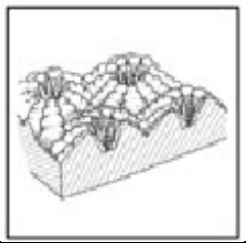
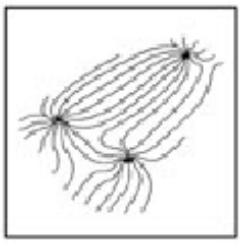
1.2.9.3. Columella meanders

	centres distinct	Colonies which have multiple mouths arranged in strict lines along valleys with collumellae occuring along valleys but in discrete centres.
	centres indistinct	Colonies which have multiple mouths aligned along valleys with columellae forming indistinct centres.
	columella continuous	Colonies which have multiple mouths arranged in strict lines along a valley where collumellae are continuous along valley floors and do not form distinct ot indistinct centres

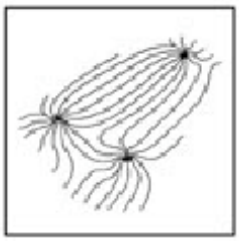
1.2.10. Septo-costae morphology

The septo-costae are radial features of the corallite. Within the corallite wall the radial elements are known as septa and outside the wall they are known as costae.

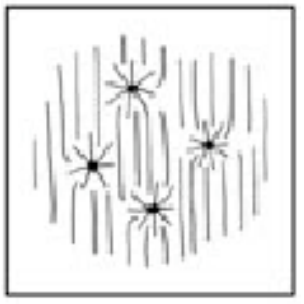
1.2.10.1. Septo-costae presence

	State	**Description**
	costae absent	Taxa with no costae. This state is common in Porites and Montipora and in species with adjoining walls (cerioid or meandroid).
	costae distinct from septa	Septa and costae are distinct structures.
	septa and costae indistinguishable	Septo-costae are single structures which are not divisible into separate septa and costae either because there is no clearly defined wall, or because of a lack of morphological distinctions. This state is common in the Agariciidae, some Pectiniidae, Siderastreiidae and colonial fungiids

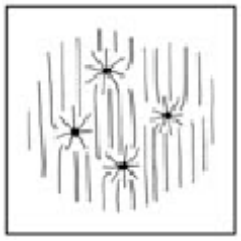
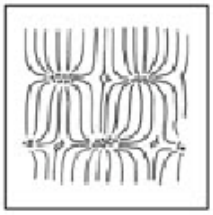
1.2.10.2. Costae dominance over septae

	State	Description
	costae dominant over septa	Costae, or the costal component of septo-costae, are more conspicuous or dominant than septa.
	costae not dominant over septa	Costae, or the costal component of septo-costae, are not more conspicuous or dominant than septa

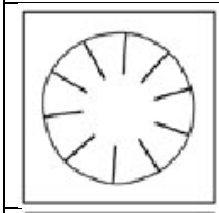
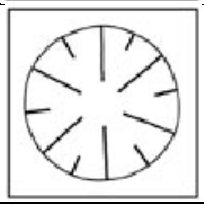
1.2.10.3. Symmetry of the septocostae

	State	Description
	bilateral	Colonies or individuals where septa have a bilateral symmetry either side of the long axis of one or many mouths. Septa are bilaterally symmetrical either side of valleys in meandroid and flabello-meandroid corals or either side of the oral groove in fungiids
	parallel	Taxa in which radial symmetry around corallite centres is absent or very indistinct, and walls or collines are also indistinct or absent, such that bilateral symmetry is absent and the surface appears to be wholly dominated by parallel septo-costae. This state is extremely rare.
	radial	Taxa where the radial symmetry of septa and/or septo-costae is overwhelmingly dominant in the mature colony. This state is found in the majority of taxa. All septo-costae are initially radially symmetrical, but this symmetry may be lost in subsequent growth
	radial and bilateral parallel	Taxa in which there is a clear coexistence of both radial and parallel or bilateral symmetries.

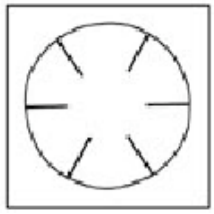
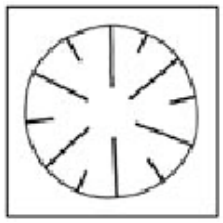
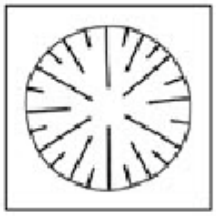
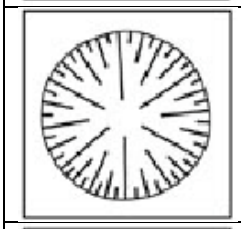
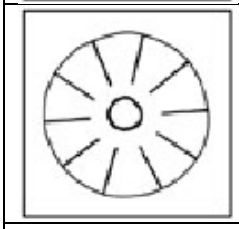
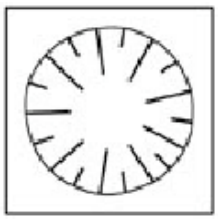
1.2.10.4. Symmetry of septocostae mixed

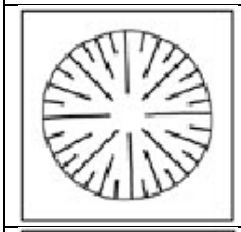
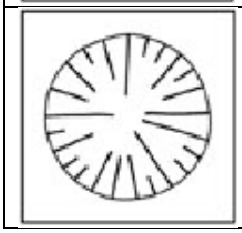
	State	Description
	radial and bilateral	Colonies in which radial and bilateral symmetries are similarly dominant. A relatively uncommon state that includes some submeandroid taxa and a number of taxa with both round and elongate corallites.
	radial and parallel	Costae are parallel and continuous around corallites, but septa are distinctly radial. An uncommon state occurring in some Agariciidae and a few taxa from other families.
	strongly parallel	Septo-costae are not wholly radial from the corallite centre but instead form a spider-like arrangement, half going in one direction and half in the opposite direction. This state is common in the Agariciidae but otherwise is found in only a few taxa.

1.2.10.5. Septal length

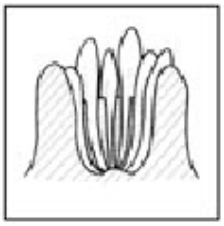
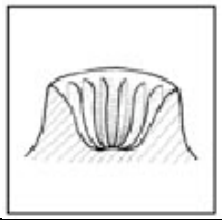
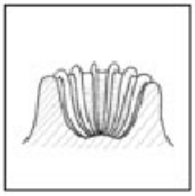
	State	
	mostly equal	Colonies where septa within the same corallite or valley are all of approximately similar length.
	unequal	Colonies where septa within the same corallite or valley are not all of uniform length. Septa are clearly not of uniform length. The majority of taxa have this state

1.2.10.6. Cycles of septa

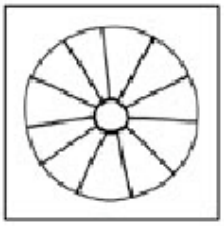
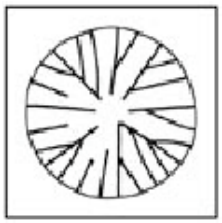
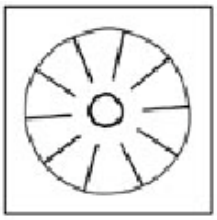
	State	Description
	1 cycle	Colonies in which corallites have only six septa. Found only in species with small corallites. Commonly seen only in *Montipora*, *Acropora* and *Seriatopora* when no second cycle is distinguishable.
	2 cycles	Colonies with corallites which mostly have 12 septa, generally arranged in one cycle of six long septa alternating with a second cycle of six shorter or sometimes only rudimentary septa. Most *Acropora*, *Montipora* and *Seriatopora* have two cycles although, in some colonies, only one may be distinguished.
	3 cycles	Septa are present in two cycles of six and a third of 12.
	> 3 cycles	Corallites with numerous septa which have a cyclical arrangement, with more than three lengths. This state is rarely well-defined
	1 order	Colonies which are dominated by corallites which have septa of equal length but more than six in number
	2 alternating orders	Colonies which are dominated by corallites which have two alternating series of septa, each numbering more than six. When this state is well developed, long septa reach the columella and short septa remain close to the wall.

	State	Description
	≥3 orders	Colonies are dominated by corallites in which septa are arranged in three or more orders, each of which numbers more than six. This state is commonly indistinct.
	irregular lengths	Septa are irregular and non-cyclical or which form a non-alternating pattern. This state is common in *Poritidae*, *Mussidae* and in a number of *Faviidae*.

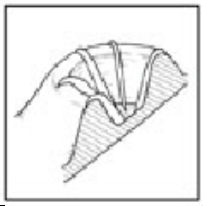
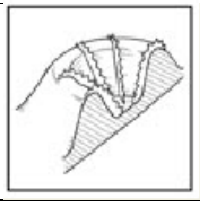
1.2.10.7. Septal height

	State	Description
	conspicuously exert	Taxa in which at least some of the septa are conspicuously exsert, reaching a height above the wall of approximately three times the median distance between the septa at the edge of the corallite wall. This state occurs predominantly in large and middle-sized corallites.
	not exsert	Septa do not project above the wall or colony surface and are inconspicuous.
	slightly to moderately exsert	Taxa in which septa project above the corallite wall but the height of septa above the wall does not reach three times the median distance between septa at the wall edge. No septa are conspicuously exsert. This is a very common state

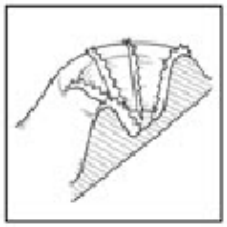
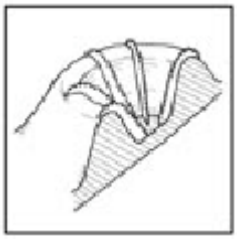
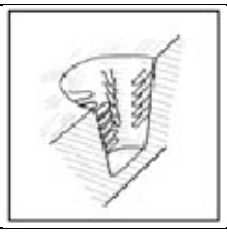
1.2.10.8. Septal fusion

	State	Description
	fused at or with columella	Colonies in which a majority of corallites have septa which can be seen (with a hand lens but without sectioning the skeleton) to fuse at or with the columella.
	fused with other septa	Corallites where septa are fused together independently of their fusion with a columella. This state is common only in *Poritidae* and *Siderastreidae* but occurs sporadically in other groups.
	not fused	Septa have inner margins that are neither fused with each-other nor, observably, with the columella. This occurs where there are no columellae (as with all *Montipora*), where septa are short and fusion with the columella or other septa is not observable with a hand lens, and where fusion with the columella is obscured.

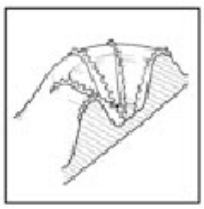
1.2.10.9. Septal margin

	State	Description
	not smooth edged	Septa which do not have smooth margins when viewed with a hand lens. This is a very common state.
	smooth edged	Septa with smooth margins to an enlargement visible with a hand lens. This is a fairly uncommon state.

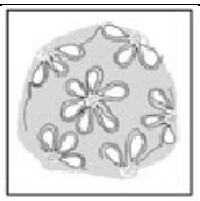
1.2.10.10. Septal dentition

	State	Description
	distinctly toothed	Septal margins have distinct teeth, the structure of which can be observed with the naked eye. This is a common state in a wide range of taxa but particularly those which have medium to very large corallites
	finely granulated or beaded	To the naked eye septa do not appear smooth but septal teeth are very fine and their structure is indistinct. This is a common state in a wide range of taxa, but particularly those with small or medium sized corallites.
	forms comb rows	Septa are reduced to vertical rows of horizontal (comb-like) inwardly projecting spines. This is a common state in *Montipora*, *Acropora*, *Anacropora* and *Alveopora.*

1.2.10.11. Distinctly toothed

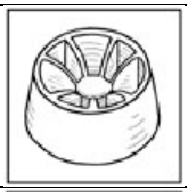
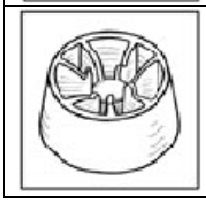
	State	Description
	teeth dominant	Septal margins have distinct teeth which are very dominant. Teeth can be sharp or blunt, but are large and dominant, generally large and well spaced, and are often irregular in height and thickness both along and between septa. This state is mostly confined to colonies with large to very large sized corallites, particularly the *Mussidae.*
	teeth not dominant	Septal margins have distinct teeth but teeth are not dominant. Teeth can be sharp or blunt, but are finely rather than coarsely serrated, relatively close together, generally regular in height and thickness and often small. This state occurs in many taxa with medium to large sized corallites, particularly in the *Faviidae*.

1.2.10.12. Septo-costae petaloid

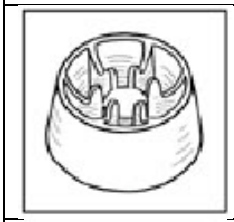
	State	Description
	fully petaloid	Corals in which finely textured skeletal material envelops a number of septo-costae such that the septo-costae appear as petaloid components of a flower-like structure.
	not petaloid	Colonies do not have septo-costae which form petaloid features, whether these form a flower-like ring or not. Most coral taxa do not have petaloid features.
	sub petaloid	Corals in which finely textured skeletal material envelops one or more septo-costae such that the septo-costae form petal-like structures, but where these do not form a distinct flower-like feature.

1.2.11. <u>Paliform structures</u>

1.2.11.1. Paliform structures present

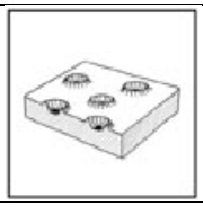
	State	Description
	absent	Taxa where there are no paliform structures present at the inner margins of septa. Paliform structures are upgrowths of septa forming vertical rods or plates located at the inner margins of septa.
	conspicuous	Paliform structures are well developed and distinct, often forming well-defined rings or crowns. Conspicuous paliform structures are commonly visible underwater.
	inconspicuous	Paliform structures are present but poorly developed with little upward growth, or which only occur on one or two septa in each corallite. Paliform structures which can only just be seen and might be microscopic.

1.2.11.2. Paliform structure type

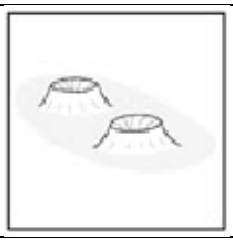
	State	Description
	laterally flattened	Vertical upgrowths forming the paliform structures are two-dimensional and laterally flattened.
	not laterally flattened	Vertical upgrowths forming the paliform structures are three-dimensional forming a club, bulb, spike or rod.

1.2.12. Inter corallite (extra-thecal) morphology

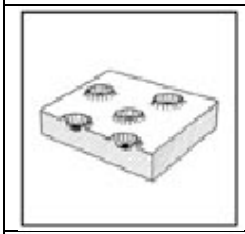
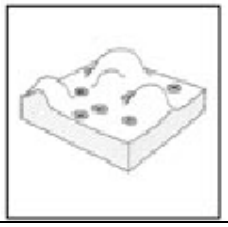
1.2.12.1. Extra-thecal skeleton

	State	Description
	absent	Colonies where the surface is covered with compact corallites or valleys, so that non-wall inter-corallite (extra-thecal) regions cannot be distinguished.
	present	Colonies in which a non-wall inter-corallite (extra-thecal) region is present.

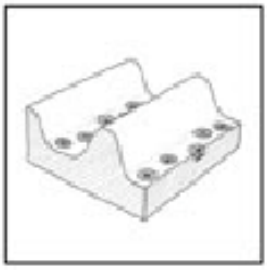
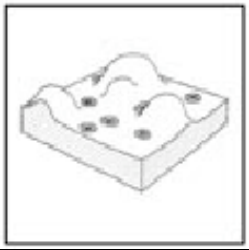
1.2.12.2. Extra-thecal surface

	State	Description
	forms blisters	The basal structure of the extra-thecal region may appear smooth in living colonies but skeletal detail shows a complex of smooth, fine, skeletal plates (dissepiments) in layers, which appear blister-like. These blisters are sometimes only just visible (i.e. *Favia lizardensis*). This skeletal state is best developed in colonies from deep or turbid water, but occurs in relatively few taxa across a range of groups.
	perforated	The basal structure of the extra-thecal skeleton is a complex of interconnected rods and spinules that creates a perforated appearance. This is a very common state.
	solid	The basal structure of the extra-thecal skeleton is smooth and uniformly solid (imperforate, generally composed of sterome), irrespective of the presence of costae and other overlying ornamentations.

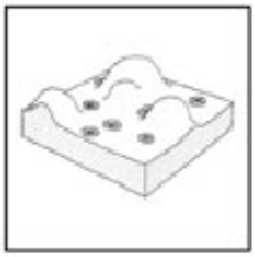
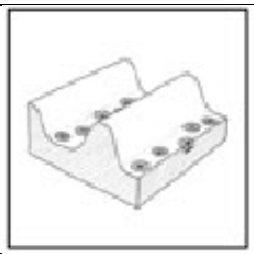
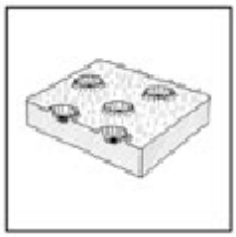
1.2.12.3. Extra-thecal elaborations

	State	Description
	absent	Colonies where the non-wall inter-corallite (extra-thecal) region has no additional structures such as costae, spines, papillae or coenosteal mounds or ridges observable with the naked eye.
	present	Colonies where the non-wall inter-corallite (extra-thecal) region has additional structures such as costae, spines, papillae or coenosteal mounds or ridges observable with the naked eye.

1.2.12.4. Linear elaborations

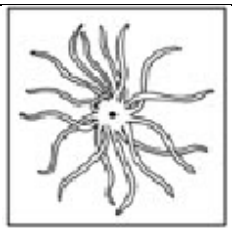
	State	Description
	larger than calice diameter	Colonies in which extra-thecal elaborations form ridges that are more than the width of the calices and where such ridges do not have corallites embedded in them (or only very rarely) nor septo-costae traversing them. This state is usually visible in living colonies and is common in *Montipora.*
	less than calice diameter	Colonies in which ridges of more than the width of calices are absent, but where ridges or elaborations of less than a calice width occur in lines in the extra-thecal region.
	none	Colonies which have no linear extra-thecal elaborations whether they are less or more than the calice size

1.2.12.5. Non-linear elaborations

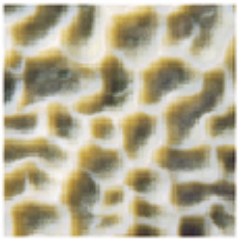
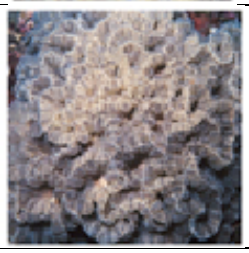
	State	Description
	larger than calice diameter	Colonies with extra-thecal elaborations of more than one calice diameter that are not arranged in lines and which do not have corallites embedded in them (or only very rarely) nor septo-costae traversing them.
	none	Colonies with no non-linear extra-thecal elaborations.
	smaller than calice diameter	Colonies where no non-linear extra-thecal elaborations of more than a calice width are present but where there are other elaborations positioned irregularly over the extra-thecal region that are less than a calice in width

1.3. Soft tissue traits

1.3.1. Tentacle length

	State	Description
	< 10 mm	Tentacles, when fully extended, are less than ten mm long and are generally thin.
	10-20 mm	Tentacles, when fully extended, are more than ten and less than 20 mm long and can be thick or thin.
	> 20 mm	Tentacles, when fully extended, are more than 20 mm long and can be thick or thin.

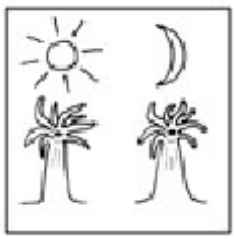
1.3.2. Skeletal masking

	State	Description
	not masked	Skeletal structures, including septal dentations and columella, are visible through tissue layers when tentacles are retracted. Very few taxa are always in this state when polyps are retracted (*Gardineroseris planulata* is an exception), but many taxa are sometimes or commonly found in this state.
	partially masked	Skeletal detail is partly obscured by tissue when tentacles are retracted. Most colonies of most taxa fall into this state.
	fully masked	Skeletal detail is obscured by tissue layers when tentacles are retracted. Texture of living tissue is very distinct.

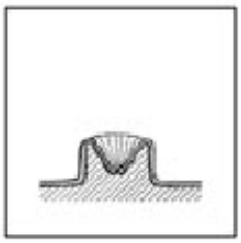
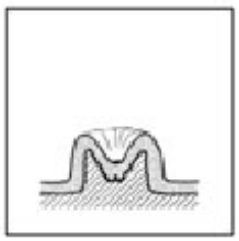
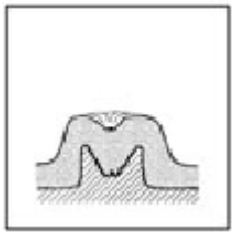
1.4. Behavioural traits

1.4.1. Feeding patterns

1.4.1.1. Day/night tissue expansion

	State	Description
	tentacles extended by day	Tentacles are extended during both the day (plus or minus three hours from solar noon) and the night. This is a common state for around 15 percent of species
	mantles extended by day	Colonies having have mantles which are extended by day. Mantles are fleshy discs which obscure the skeleton of living corals when tentacles are not extended. Mantles may be distinct from tentacles (i.e. *Trachyphyllia geoffroyi*) or be partly composed of retracted tentacles (i.e. *Blastomussa wellsi*). They typically partially retract when touched.
	vesicles extended by day	Colonies which have vesicles extended by day. The colony is covered by grape-like, bubble-like, or irregularly shaped vesicles. Vesicles may vary greatly in size (i.e. *Plerogyra* and *Physogyra*) and shape (i.e. *Physogyra lichtensteini*). Corals with vesicles have tentacles which are separate structures (usually extended only at night). Some *Euphyllia* have tentacle tips which are bubble-like and cover the colony surface (i.e. *Euphyllia yaeyamaensis*): these are not vesicles.
	no expansion by day	Colonies which do not have tentacles, mantles or vesicles extended during the day. Most corals fall into this category. All corals in this state with the exception of *Pachyseris species* (in which tentacles have never been recorded), extend tentacles at night.

1.4.1.2. Daytime tissue expansion

	State	Description
	< 1 mm	Those colonies where tissues form only a thin film over the skeleton during the day.
	1-5 mm	Some skeletal characteristics can be distinct but tissues form a layer up to five mm thick above the skeleton.
	5-20 mm	Tissues form a layer between five and 20 mm thick above the skeleton. Colonies which have extended tentacles or other tissues that protrude outwards between corallites rather than upwards. Colonies with mantles or vesicles that protrude more than five mm sideways from the edge of the corallite
	> 20 mm	Tissues project more than 20 mm from the skeleton. Tissues can include polyps, tentacles, vesicles, mantles, or fleshy tissue and can project either upwards or sideways.

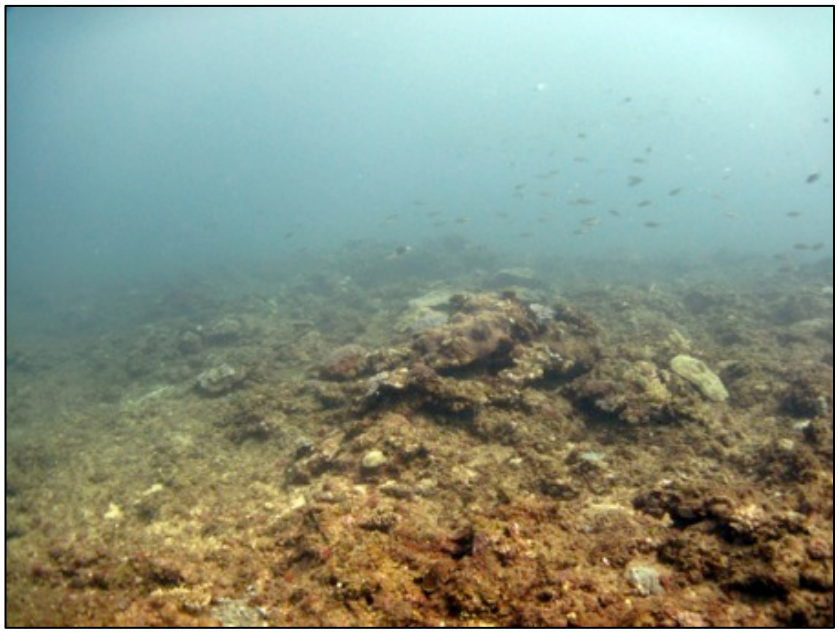
2. Reef types in Southwest Madagascar

2.1. Examples of reef types

2.1.1. Reef type M1

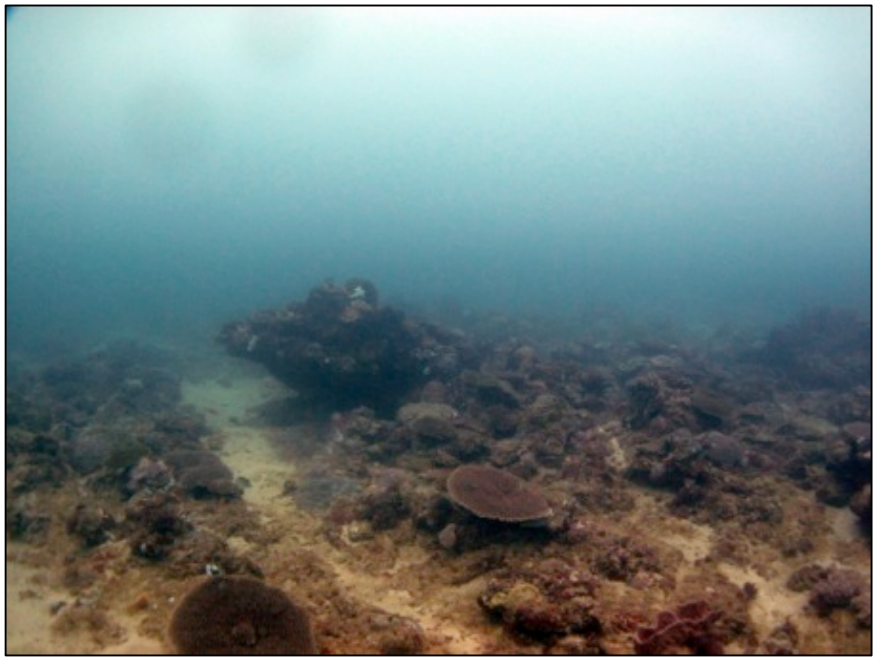
Mounded patch reef with a distinct sloped edge (site A19).

2.1.2. Reef type M2



Mounded patch reef with indistinct sloped edges (site A10).

*2.1.3. **Reef type M3***



Mounded reefs with faint sand grooves (site T13).

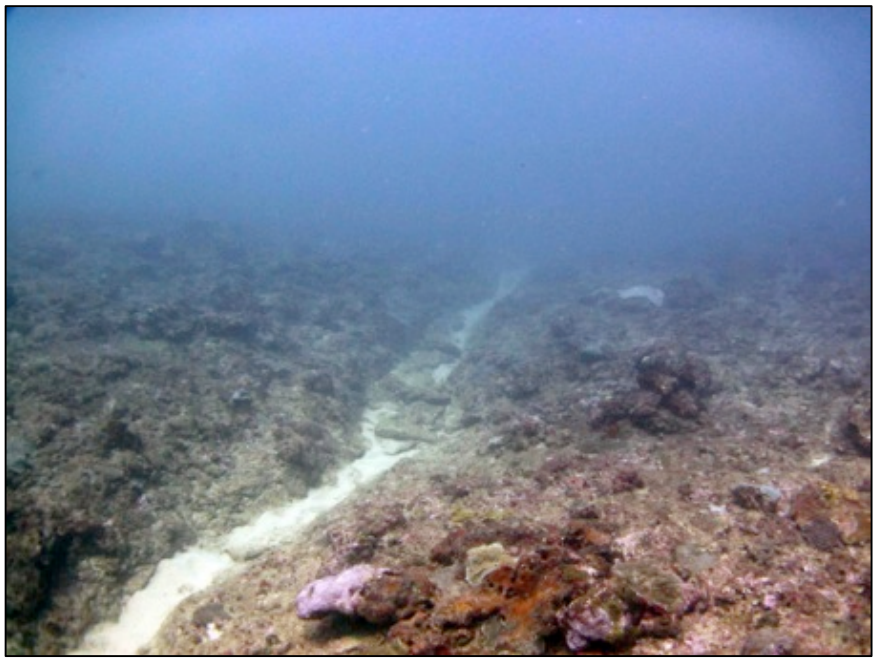
*2.1.4. **Reef type M4***

Mounded fringing reef (site A16).

*2.1.5. **Reef type M5***

A reef pillar. The image was taken on one side of the pillar (site R16).

*2.1.6. **Reef type SG1***



Shallow, narrow grooves with gently sloping spurs; grooves are occasional non-dominant features of the system (site R13).

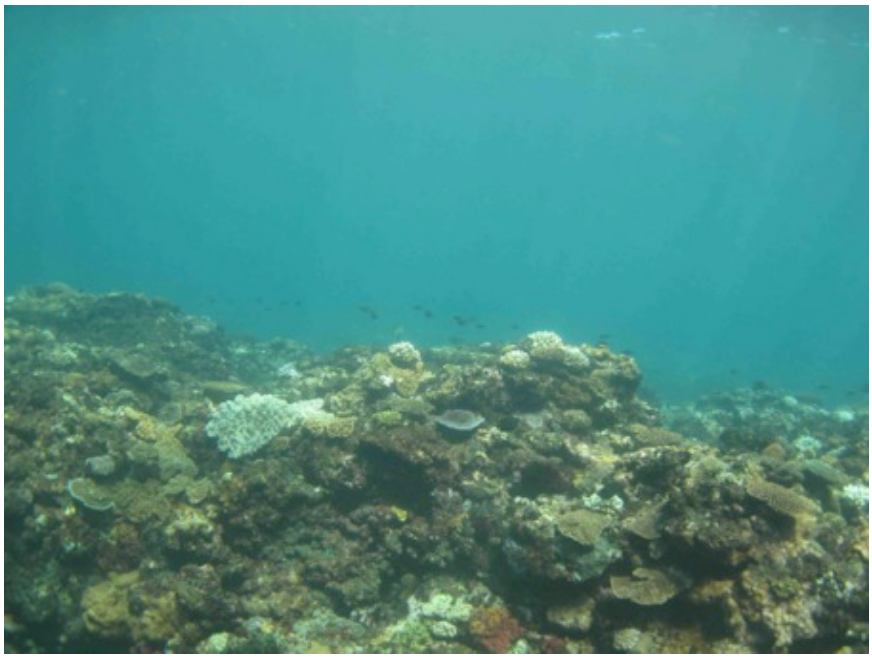
2.1.7. Reef type SG2

Spur and groove system with clearly defined grooves that are regular and prominent features in the system (site T2).

2.1.8. Reef type SG3

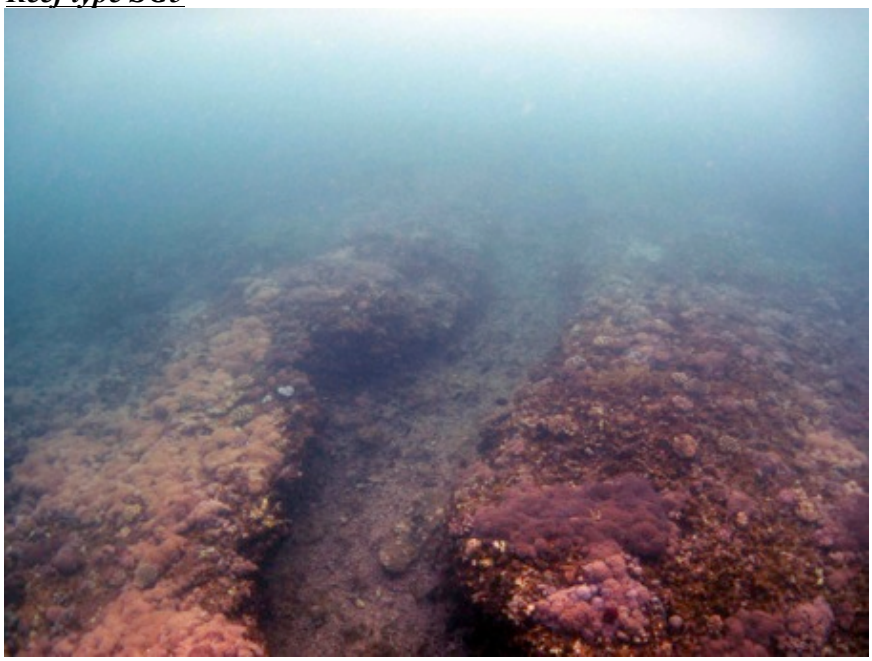
Spur and groove system characterized by blunt and bulky spurs projecting like nubby finger onto a sand bed (site T6).

2.1.9. Reef type SG4



Spur and groove system characterized by very large (ten m tall) spurs with nearly U-shaped canyon-like grooves (site R24). Image shows top of spur.

2.1.10. Reef type SG5

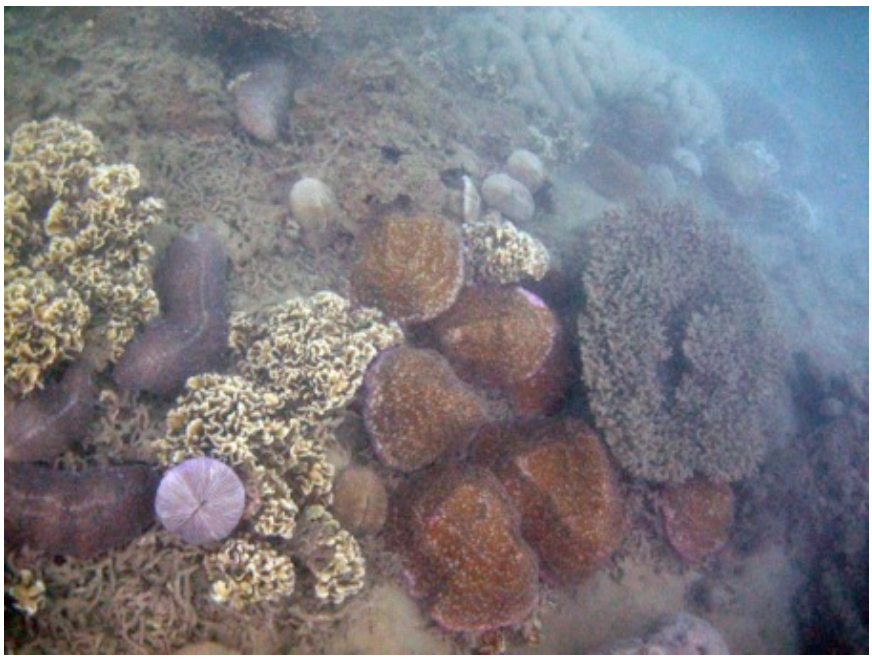


Spur and groove system where spurs consist of a framework of branching rubble solidified by coralline algae and grooves are filled with fragments of this same branching coral rubble (site A4).

2.1.11. Reef type RF1

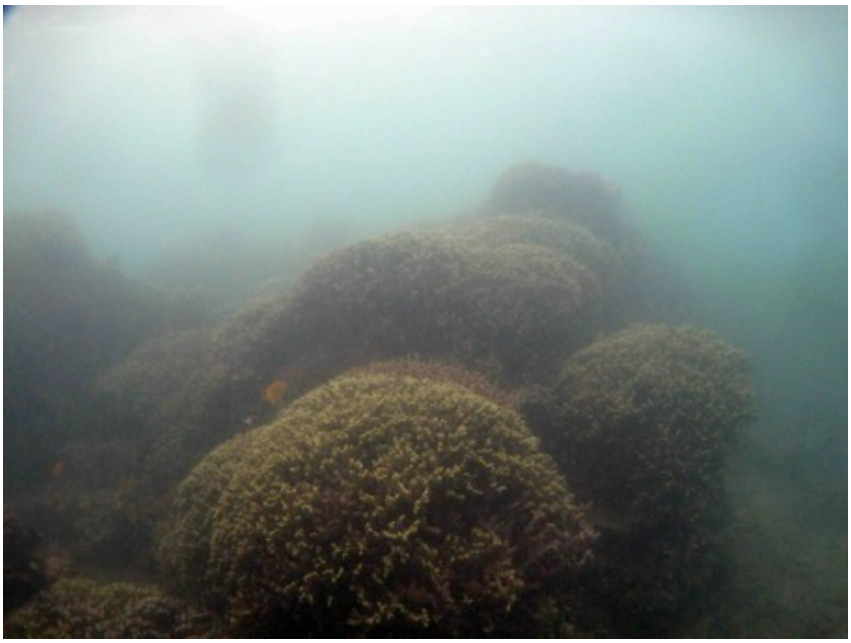
Patch ‘reef’ consisting of a meshwork of branching and foliose coral rubble (site R9)

2.1.12. Reef type RF2-lower slope



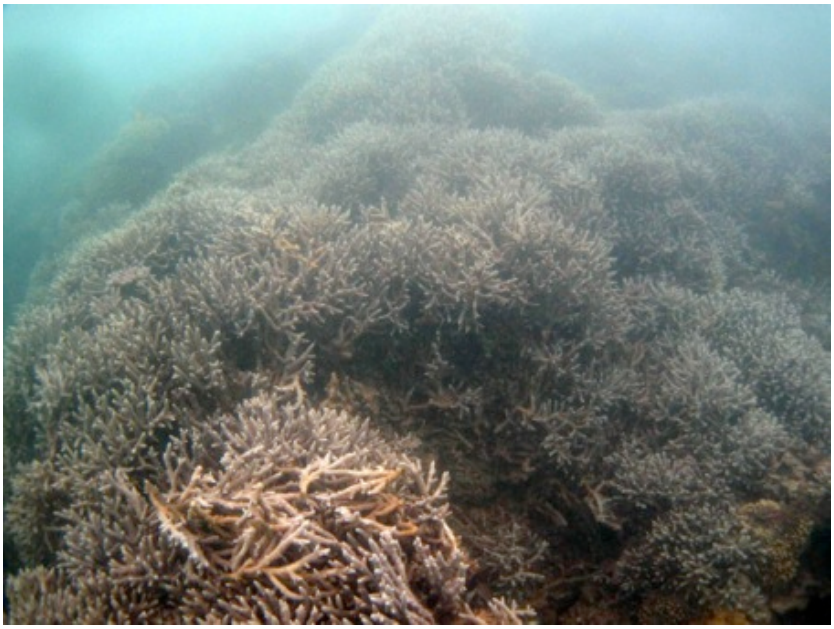
Lower slope (ten to 15 metres) of a type RF2 reef. This reef type is characterized by a sediment laden rubble slope (site T4).

2.1.13. Reef type RF2-upper slope 1



The reef flat (three to four metres) characterized by a sediment laden rubble slope. The image shows the extensive stand of *Porites rus* typical found on the reef flats this reef type (site T4).

2.1.14. Reef type RF2-upper slope 2



The reef flat (three to four metres) of a type RF2 characterized by a sediment laden rubble slope. The image shows the extensive monostand of staghorn *Acropora* sp. typical found on the reef flats this reef type (site T4).

2.1.15. Reef type RF2- mid-slope

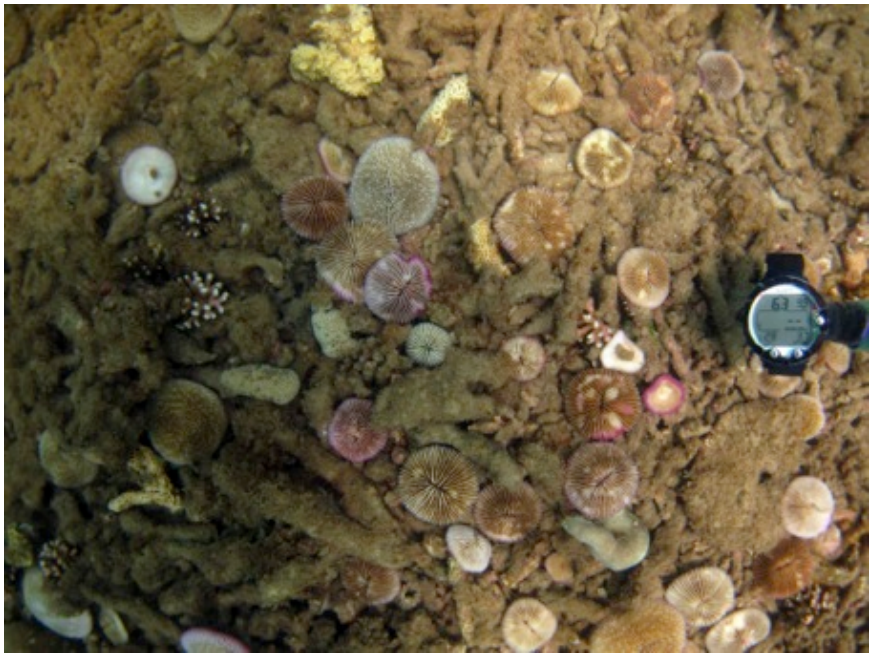
The middle reef slop (five to metres) characterized by a sediment laden rubble slope. The image shows the extensive monostand of staghorn *Acropora* sp. typical found on the reef flats this reef type (site T3).

2.1.16. Reef type CW

A coral wall. This reef type is characterized by a very steep, sometimes vertical, reef 'wall' with firm and non-movable substrate (site A28).

2.2. Features of MMR and MR features

2.2.1. Example of rubble patch



Example of a rubble patch that is inundated with *Cycloseris* spp and *Fungia* spp.

2.2.2. Example of rubble field

Example of rubble field with a pack of urchins (black).

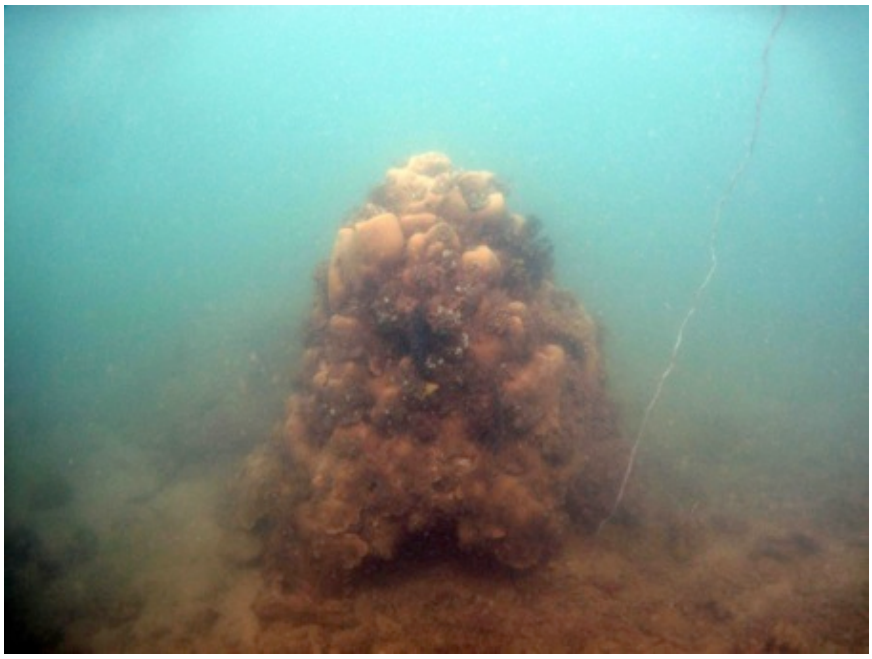
2.2.3. Example 1 of mound

Mound common in MR type and MRR type reefs.

2.2.4. Example 2 of mound

Mound common in MR type and MRR type reefs.

2.2.5. Example 3 of mound



Mound common in MR type and MRR type reefs.

2.2.6. Example of Pavona clavus monostand wall

Large mono-stand of *Pavona clavus.*

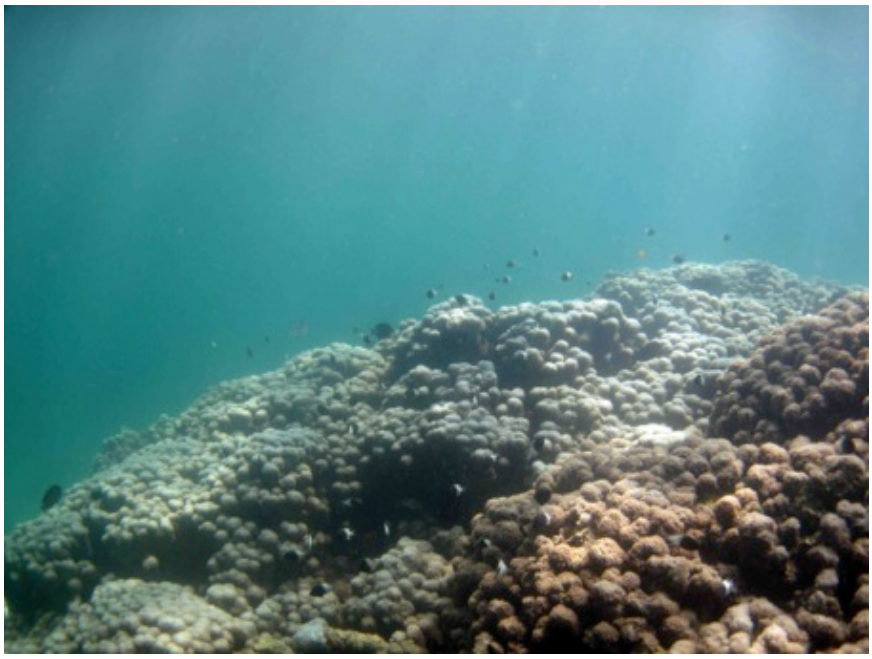
2.2.7. Example of Lobophyllia hemprichii monostand wall

Large mono-stand of *Lobophyllia hemprichii*.

2.2.8. Example of Montipora spp. monostand

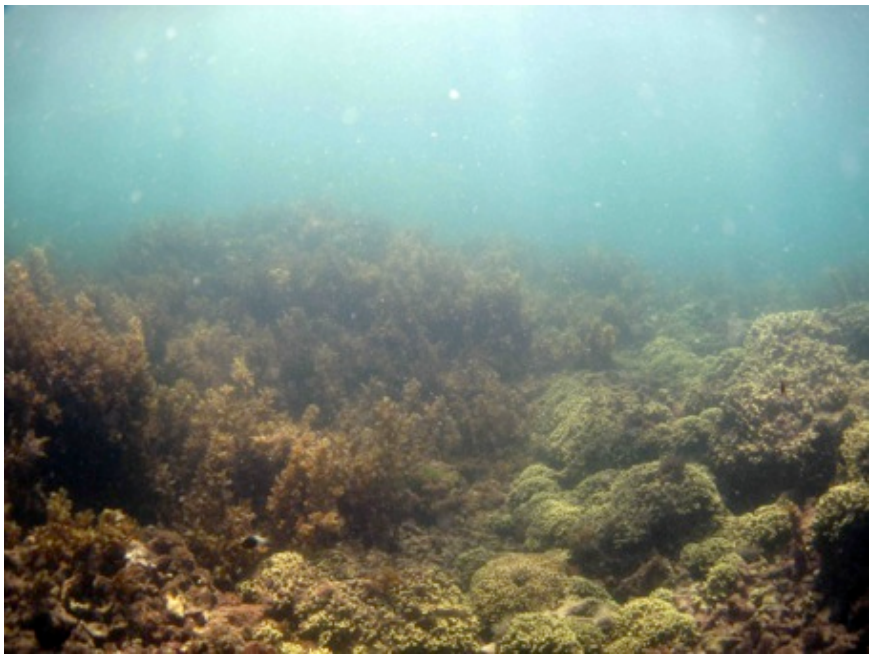
Large mono-stand of foliose *Montipora* spp.

2.2.9. Example of Galaxea astreata monostand



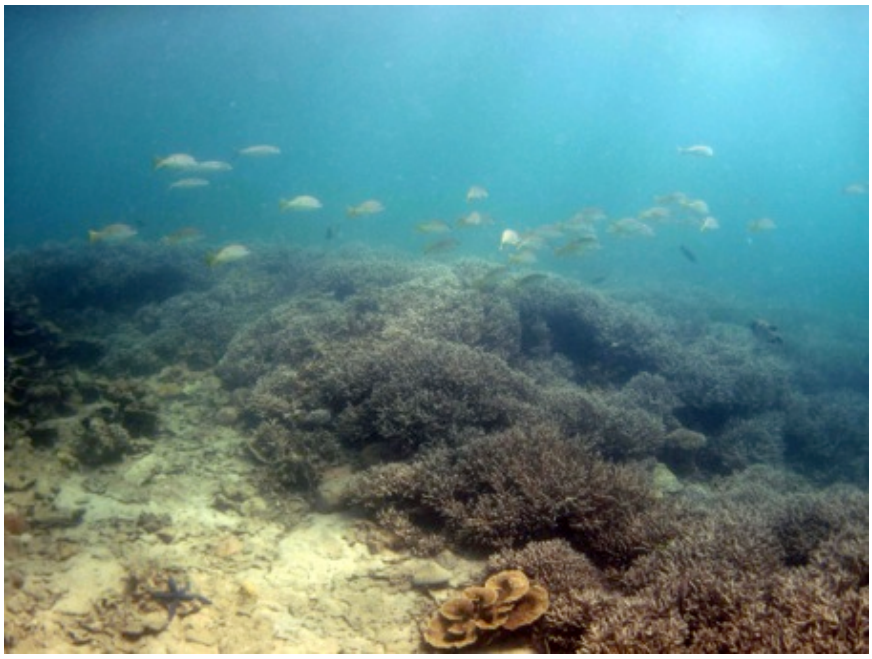
Large mono-stand of *Galaxea astreata*.

2.2.10. Example of Porites rus monostand



Large mono-stand of *Porites rus* adjacent to an encroaching field of *Turbinaria* sp.

2.2.11. Example of Acropora spp. monostand



Large mono-stand of bushy *Acropora* sp. adjacent to a rubble field.

3. CPCe code file

The following is the text file used for the CPCe identification of coral species and clusters in this study. NB this text file is available electronically as Digital Supplement 1.2.

```
68
"C","Coral"
"ACAN","Acanthastrea"
"ACR","Acropora"
"ALV","Alveopora"
"ANA","Anacropora"
"ANO","Anomastraea"
"AST", "Astreopora"
"BLA","Blastomusa"
"COE","Coeloseris"
"COSC","Coscinarea"
"CYCL","Cycloseris"
"CYPH","Cyphastrea"
"DIP","Diploastrea"
"EPHY","Echinophyllia"
"EPOR","Echinopora"
"EUP","Euphyllia"
"FAVA","Favia"
"FAVT","Favites"
"FUN", "Fungia"
"GAL","Galaxea"
"GARD","Gardineroseris"
"GON","Goniastrea"
"GONP","Goniopora"
"GYR","Gyrosmilia"
"HALO","Halomitra"
"HEL","Heliopora"
"HER","Herpolitha"
"HET","Heteropsammia"
"HOR","Horastrea"
"HYD","Hydnophora"
"LPTA","Leptastrea"
"LPTO","Leptoria"
"LPTS","Leptoseris"
"LBP","Lobophyllia"
"MER","Merulina"
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"MIL","Millepora"
"MNTA","Montastrea"
"MNTI","Montipora"
"MYCE","Mycedium"
"OUL","Oulophyllia"
"OXY","Oxypora"
"PACH","Pachyseris"
"PAV","Pavona"
"PECT","Pectinia"
"PHYS","Physogyra"
"PLER","Plerogyra"
"PLAT","Platygyra"
"PLES","Plesiastrea"
"POC","Pocillopora"
"PODA","Podabacia"
"POLY","Polyphyllia"
"POR","Porites"
"PSAM","Psammocora"
"SERI","Seriatopora"
"SIDE","Siderastrea"
"STYL","Stylophora"
"SMP","Symphyllia"
"TURB","Turbinaria"
"TUBI","Tubipora"
"TUBIA","Tubiastrea sp"
"SC","Soft Coral"
"BC","Black coral"
"SP","Sponges"
"OT","OtherLife form"
"A","Algae"
"S","Substrate"
"UK","Unknown"
"TWS","Tape,wand,shadow"
"ACB","Acanthastrea brevis","ACAN"
"ACE","Acanthastrea echinata","ACAN"
"ACH","Acanthastrea hemprichii","ACAN"
"ACI","Acanthastrea ishigakiensis","ACAN"
"ACL","Acanthastrea lordhowensis","ACAN"
"ACRT","Acropora tables and plates","ACR"
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"ACRST","Acropora Staghorn","ACR"
"ACRB","Acropora bushy","ACR"
"ACRS","Acropora submassive","ACR"
"ACRBO","Acropora bottle brush","ACR"
"ACRC","Acropora corymbose","ACR"
"ACRD","Acropora digitate","ACR"
"ACRE","Acropora encrusting","ACR"
"ALA","Alveopora allingi","ALV"
"ALD","Alveopora daedalea","ALV"
"ALF","Alveopora fenestrata","ALV"
"ALS","Alveopora spongiosa","ALV"
"ALT","Alveopora tizardi","ALV"
"ANF","Anacropora forbesi","ANA"
"ANI","Anomastraea irregularis","ANO"
"ASL","Astreopora listeri","AST"
"ASM","Astreopora myriophthalma","AST"
"ASO","Astreopora ocellata","AST"
"BLM","Blastomussa merleti","BLA"
"COM","Coeloseris mayeri","COE"
"COC","Coscinaraea columna","COSC"
"COCR","Coscinaraea crassa","COSC"
"COMO","Coscinaraea monile","COSC"
"CYSP","Cycloseris sp","CYCL"
"CYC","Cyphastrea chalcidium","CYPH"
"CYM","Cyphastrea microphthalma","CYPH"
"CYS","Cyphastrea serailia","CYPH"
"DIPL","Diplostrea heliopora","DIP"
"ECA","Echinophyllia aspera","EPHY"
"ECE","Echinophyllia echinata","EPHY"
"ECO","Echinophyllia orpheensis","EPHY"
"ECF","Echinopora forskaliana","EPOR"
"ECG","Echinopora gemmacea","EPOR"
"ECH","Echinopora hirsutissima","EPOR"
"ECL","Echinopora lamellosa","EPOR"
"EUG","Euphyllia glabrescens","EUP"
"FAF","Favia favus","FAVA"
"FAH","Favia helianthoides","FAVA"
"FAL","Favia lizardensis","FAVA"
"FAM","Favia maritima","FAVA"
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"FAPA","Favia pallida","FAVA"
"FAMA","Favia matthaii","FAVA"
"FAR","Favia rotumana","FAVA"
"FAS","Favia speciosa","FAVA"
"FAST","Favia stelligera","FAVA"
"FAV","Favia veroni","FAVA"
"FAA","Favites abdita","FAVT"
"FAC","Favites chinensis","FAVT"
"FACO","Favites complanata","FAVT"
"FAFL","Favites flexuosa","FAVT"
"FAHA","Favites halicora","FAVT"
"FAPE","Favites pentagona","FAVT"
"FARU","Favites russelli","FAVT"
"FAVA","Favites vasta","FAVT"
"FUNSP","Fungia species","FUN"
"DIDI","Diaseris distorta","FUN"
"DIFR","Diaseris fragilis","FUN"
"GAA","Galaxea astreata","GAL"
"GAF","Galaxea fascicularis","GAL"
"GAP","Gardineroseris planulata","GARD"
"GOA","Goniastrea aspera","GON"
"GOAU","Goniastrea australensis","GON"
"GOE","Goniastrea edwardsi","GON"
"GOMI","Goniastrea minuta","GON"
"GOPA","Goniastrea palauensis","GON"
"GOPE","Goniastrea pectinata","GON"
"GOPER","Goniastrea peresi","GON"
"GOR","Goniastrea retiformis","GON"
"GOAL","Goniopora albiconus","GON"
"GOB","Goniopora burgosi","GONP"
"GOC","Goniopora columna","GONP"
"GOD","Goniopora djiboutiensis","GONP"
"GOL","Goniopora lobata","GONP"
"GOM","Goniopora minor","GONP"
"GOP","Goniopora planulata","GONP"
"GOS","Goniopora somaliensis","GONP"
"GOST","Goniopora stokesi","GONP"
"GOT","Goniopora tenuidens","GONP"
"GYI","Gyrosmilia interrupta","GYR"
"HAP","Halomitra pileus","HALO"
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"HEC","Heliopora coerulea","HEL"
"HEL","Herpolitha limax","HER"
"HEW","Herpolitha weberi","HER"
"HECO","Heteropsammia cochlea","HET"
"HEE","Heteropsammia eupsammides","HET"
"HOI","Horastrea indica","HOR"
"HYE","Hydnophora exesa","HYD"
"HYM","Hydnophora microconos","HYD"
"HYR","Hydnophora rigida","HYD"
"LEA","Leptastrea aequalis","LPTA"
"LEB","Leptastrea bottae","LPTA"
"LEP","Leptastrea purpurea","LPTA"
"LET","Leptastrea transversa","LPTA"
"LEPH","Leptoria phrygia","LPTO"
"LEE","Leptoseris explanata","LPTS"
"LEH","Leptoseris hawaiiensis","LPTS"
"LEI","Leptoseris incrustans","LPTS"
"LEM","Leptoseris mycetoseroides","LPTS"
"LES","Leptoseris scabra","LPTS"
"LEY","Leptoseris yabei","LPTS"
"LOC","Lobophyllia corymbosa","LBP"
"LOH","Lobophyllia hemprichii","LBP"
"MEA","Merulina ampliata","MER"
"MES","Merulina scabricula","MER"
"MIL","Millepora dichotoma","MIL"
"MIE","Millepora exesa","MIL"
"MII","Millepora intricata","MIL"
"MIP","Millepora platyphylla","MIL"
"MIT","Millepora tenera","MIL"
"MOA","Montastrea annuligera","MNTA"
"MOC","Montastrea colemani","MNTA"
"MOCU","Montastrea curta","MNTA"
"MOMG","Montastrea magnistella","MNTA"
"MOV","Montastrea valenciennesi","MNTA"
"MOL","Montipora laminar","MNTI"
"MOCO","Montipora columnar","MNTI"
"MOS","Montipora submassive","MNTI"
"MOM","Montipora massive","MNTI"
"MOF","Montipora foliose","MNTI"
"MON","Montipora encrusting","MNTI"
"MYE","Mycedium elephantotus","MYCE"
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"MYM","Mycedium mancaoi","MYCE"
"OUC","Oulophyllia crispa","OUL"
"OXL","Oxypora lacera","OXY"
"PAS","Pachyseris speciosa","PACH"
"PAB","Pavona bipartita","PAV"
"PACA","Pavona cactus","PAV"
"PAC","Pavona clavus","PAV"
"PADE","Pavona decussata","PAV"
"PADU","Pavona duerdeni","PAV"
"PAE","Pavona explanulata","PAV"
"PAF","Pavona frondifera","PAV"
"PAM","Pavona maldivensis","PAV"
"PAVV","Pavona varians","PAV"
"PAVE","Pavona venosa","PAV"
"PEA","Pectinia africanus","PECT"
"PEL","Pectinia lactuca","PECT"
"PHL","Physogyra lichtensteini","PHYS"
"PLA","Platygyra acuta","PLAT"
"PLC","Platygyra carnosus","PLAT"
"PLCR","Platygyra crosslandi","PLAT"
"PLDA","Platygyra daedalea","PLAT"
"PLL","Platygyra lamellina","PLAT"
"PLP","Platygyra pini","PLAT"
"PLR","Platygyra ryukyuensi","PLAT"
"PLS","Platygyra sinensis","PLAT"
"PLG","Plerogyra sinuosa","PLER"
"PLV","Plesiastrea versipora","PLES"
"POD","Pocillopora damicornis","POC"
"POE","Pocillopora eydouxi","POC"
"POI","Pocillopora indiania","POC"
"POV","Pocillopora verrucosa","POC"
"POC","Podabacia crustacea","PODA"
"POT","Polyphyllia talpina","POLY"
"POL","Porites latistella","POR"
"POLI","Porites lichen","POR"
"POM","Porites monticulosa","POR"
"POP","Porites profundus","POR"
"POPA","Poritipora paliformi","POR"
"POR","Porites rus","POR"
"POS","Porites sillimaniana","POR"
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"POMA","Porites massive (solida, lobata, lutea)","POR"
"PSC","Psammocora contigua","PSAM"
"PSE","Psammocora explanulata","PSAM"
"PSH","Psammocora haimeana","PSAM"
"PSN","Psammocora nierstraszi","PSAM"
"PSP","Psammocora profundacella","PSAM"
"PSS","Psammocora superficialis","PSAM"
"SEC","Seriatopora caliendrum","SERI"
"SEG","Seriatopora guttatus","SERI"
"SEH","Seriatopora hystrix","SERI"
"SIS","Siderastrea savignyana","SIDE"
"STP","Stylophora pistillata","STYL"
"STS","Stylophora subseriata","STYL"
"STW","Stylophora wellsi","STYL"
"SYA","Symphyllia agaricia","SMP"
"SYR","Symphyllia recta","SMP"
"SYV","Symphyllia valenciennesii","SMP"
"TUI","Turbinaria irregularis","TURB"
"TUM","Turbinaria mesenterina","TURB"
"TUR","Turbinaria reniformis","TURB"
"TUS","Turbinaria stellulata","TURB"
"TUB","Tubiastrea sp.","TUBIA"
"TUBM","Tubipora musica","TUBI"
"J","Juvenile <2.5cm","C"
"LC","Leather Corals Alcyoniidae","SC"
"ARBC","Arborescent Octocorals Nephtheidae and Nidaliidae","SC"
"GSFSW","Gorgonians Sea fans SeaWhips","SC"
"XNIA","Xeniidae","SC"
"BLKC", "Black coral","BC"
"SPBR","Branching Sponges","SP"
"SPEL","Encrusting or lumpy sponges","SP"
"SPC","Sponge cups","SP"
"ZO","Zoanthids","OT"
"FI","Fish","OT"
"AS","Ascidians tunicates sea squits","OT"
"HY","Hydroids","OT"
"ANEM","Anemones","OT"
"OTH","Giant clams, borers etc","OT"
"TA","Turf Algae","A"
"SMA","Short Macro Algae (<10cm)","A"
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"TMA","Tall Macro ALgae (>10cm)","A"
"CA","Coralline encrusting algae","A"
"BRA","Branched coralline red algae","A"
"BAC","Brown algal crusts","A"
"BT","Brown turf","A"
"HA","Halimeda","A"
"PAD","Padina","A"
"Sa","Sand","S"
"Si","Silt >5cm deep","S"
"BCRE","Branching Coral Rubble in encrusting algae","S"
"BCSE","Branching Coral Structure in encrusting algae","S"
"BCRT","Branching Coral Rubble in turf algae","S"
"BCST","Branching Coral Structure in turf algae","S"
"UNK","Unknown","UK"
"TAPE","Tape","TWS"
"WAND","Wand","TWS"
"SHAD","Shadow","TWS"

NOTES,NOTES,NOTES
"BL","Bleached coral point","NA"
"WBD","White Band Disease","NA"
"PBD","Pink Band Disease","NA"
"AC","Ask Charles","NA"
```

4. Number of images available by site and depth category

This is a summary of the images available by site and depth zone for the reefs surveyed in Southwest Madagascar between September 2009 and March 2010. While all images were not used in the analysis they do act as a photo-database of the reef condition for this region and time period that could potentially be used in future studies.

Site name	0-2 m	2-5 m	5-8 m	8-15 m	15-26 m	26-35 m	Total
A01	0	81	17	0	0	0	**98**
A02	0	62	70	32	0	0	**164**
A03	0	0	57	93	0	0	**150**
A04	0	0	116	0	0	0	**116**
A05	4	32	20	59	0	0	**115**
A06	0	39	52	45	0	0	**136**
A07	0	0	100	53	0	0	**153**
A08	0	0	5	83	17	0	**105**
A09	0	0	11	48	23	0	**82**
A10	0	0	0	60	31	0	**91**
A11	0	0	0	0	58	22	**80**
A12	0	0	0	135	0	0	**135**
A13	0	22	124	44	0	0	**190**
A14	0	0	34	64	0	0	**98**
A15	0	0	0	117	0	0	**117**
A16	0	23	76	47	0	0	**146**
A17	0	1	36	25	0	0	**62**
A18	1	33	39	16	0	0	**89**
A19	0	0	84	3	0	0	**87**
A20	0	97	19	0	0	0	**116**
A21	0	0	82	263	2	0	**347**
A22	0	0	53	28	24	0	**105**
A23	0	0	0	74	0	0	**74**
A24	0	0	0	177	34	0	**211**
A25	0	0	0	29	32	0	**61**
A26	0	0	0	107	23	0	**130**
A27	0	18	33	62	0	0	**113**
A28	0	68	29	26	0	0	**123**
A29	0	0	0	0	49	0	**49**
A30	0	0	0	0	66	65	**131**
R01	3	46	49	0	0	0	**98**
R02	10	61	55	0	0	0	**126**
R03	0	0	0	47	3	0	**50**

Site name	0-2 m	2-5 m	5-8 m	8-15 m	15-26 m	26-35 m	Total
R04	0	0	17	45	0	0	**62**
R05	2	25	1	0	0	0	**28**
R06	24	58	12	0	0	0	**94**
R07	0	118	8	0	0	0	**126**
R08	2	64	3	0	0	0	**69**
R09	2	76	0	0	0	0	**78**
R10	0	0	23	46	0	0	**69**
R11	0	0	0	56	6	0	**62**
R12	0	0	0	0	50	0	**50**
R13	0	0	0	0	47	0	**47**
R14	0	0	0	0	65	0	**65**
R15	0	0	11	92	1	0	**104**
R16	0	0	23	49	0	0	**72**
R17	26	27	2	0	0	0	**55**
R19	42	84	0	0	0	0	**126**
R20	10	49	1	0	0	0	**60**
R21	0	8	11	6	0	0	**25**
R22	0	65	0	0	0	0	**65**
R23	0	0	0	0	47	0	**47**
R24	0	9	17	49	1	0	**76**
T01	0	18	0	0	0	0	**18**
T02	0	0	28	35	18	0	**81**
T03	0	38	39	76	0	0	**153**
T04	0	49	27	53	0	0	**129**
T05	0	0	0	51	22	0	**73**
T06	0	8	52	49	0	0	**109**
T07	19	63	7	0	0	0	**89**
T08	0	57	107	4	0	0	**168**
T09	3	47	66	7	0	0	**123**
T10	5	30	53	58	0	0	**146**
T11	0	21	66	28	0	0	**115**
T12	0	0	1	85	0	0	**86**
T13	0	0	19	151	18	0	**188**
T14	0	47	0	0	0	0	**47**
Total	**153**	**1544**	**1755**	**2677**	**637**	**87**	**6853**

5. Commonality of species

The global commonality of species used to determine weighting of species in the species cluster replacement method detail in Section 4.3.

Species	Commonality used for weighting	Weighting	Commonality based on Carpenter et al. 2009	Commonality based on Veron 2000	Commonality Veron 2000 verbatum
Acropora abrotanoides	Sometimes common	0.3	Uncommon	Sometimes common	Sometimes common
Acropora aculeus	Uncommon	0.1	Uncommon	Uncommon	Usually common in the central Indopacific, uncommon elsewhere
Acropora anthocercis	Sometimes common	0.3	Uncommon	Sometimes common	Sometimes common
Acropora appressa	Common	0.55	Uncommon	Common	Common in the western Indian Ocean, uncommon elsewhere
Acropora arabensis	Common	0.55	Common	Not Clear	Locally common
Acropora austera	Uncommon	0.1	Common	Uncommon	Usually uncommon
Acropora branchi	Common	0.55	NA	Common	Common
Acropora brueggemanni	Common	0.55	NA	Common	Common
Acropora cerealis	Common	0.55	Common	Common	Common
Acropora clathrata	Common	0.55	Common	Common	Common
Acropora copiosa	Rare	0.05	NA	Rare	Uncommon in Japan, rare elsewhere
Acropora cuneata	Common	0.55	NA	Common	Common
Acropora cytherea	Common	0.55	Common	Common	Common but conspicuous
Acropora digitifera	Uncommon	0.1	Uncommon	Uncommon	Uncommon except on some sheltered reef slopes

Species	Commonality used for weighting	Weighting	Commonality based on Carpenter et al. 2009	Commonality based on Veron 2000	Commonality Veron 2000 verbatum
Acropora divaricata	Common	0.55	Common	Common	Common, may be a dominant species
Acropora florida	Common	0.55	Common	Common	Common
Acropora formosa	Common	0.55	Common	Common	Common and frequently a dominant species
Acropora forskali	Uncommon	0.1	NA	Uncommon	Uncommon
Acropora gemmifera	Common	0.55	Common	Common	Common
Acropora glauca	Common	0.55	Rare	Common	Common in subtropical locations rare elsewhere
Acropora grandis	Common	0.55	Common	Common	Common
Acropora granulosa	Common	0.55	Common	Common	Common
Acropora hemprichii	Common	0.55	Common	Common	Common
Acropora horrida	Uncommon	0.1	Uncommon	Uncommon	Usually uncommon
Acropora humilis	Common	0.55	Common	Common	Usually common, and sometimes a dominant species
Acropora hyacinthus	Common	0.55	Common	Not Clear	One of the most abundant corals of exposed outer reef slopes of much of the western Pacific.
Acropora inermis	Uncommon	0.1	NA	Uncommon	Uncommon
Acropora irregularis	Sometimes Common	0.3	NA	Sometimes common	Sometimes common, especially in the western Indian Ocean
Acropora lamarcki	Common	0.55	NA	Common	Common

Species	Commonality used for weighting	Weighting	Commonality based on Carpenter et al. 2009	Commonality based on Veron 2000	Commonality Veron 2000 verbatum
Acropora latistella	Rare	0.05	Common	Rare	Common excepty in the central and western Indian Ocean where it is only known from a few records
Acropora longicyathus	Common	0.55	Common	Common	Common and may be dominant species on unconsolidated substrates
Acropora loripes	Common	0.55	Common	Not Clear	Common in the central Indo-Pacific
Acropora macrostoma	Uncommon	0.1	NA	Uncommon	Common in Indonesia, uncommon elsewhere.
Acropora microphthalma	Common	0.55	Common	Common	Common and may be a dominant species in shallow water
Acropora millepora	Common	0.55	Common	Common	Common
Acropora mirabilis	Sometimes common	0.3	NA	Sometimes common	Sometimes common
Acropora monticulosa	Uncommon	0.1	Uncommon	Uncommon	Sometimes common in eastern Austalia, usually uncommon elsewhere
Acropora nana	Sometimes common	0.3	Uncommon	Sometimes common	Sometimes common
Acropora nasuta	Common	0.55	Common	Common	Common
Acropora natalensis	Uncommon	0.1	NA	Uncommon	Uncommon
Acropora nobilis	Common	0.55	Common	Common	Common
Acropora ocellata	Rare	0.05	NA	Rare	Rare

Species	Commonality used for weighting	Weighting	Commonality based on Carpenter et al. 2009	Commonality based on Veron 2000	Commonality Veron 2000 verbatum
Acropora palifera	Sometime common	0.3	NA	Sometime common	The most abundant coral of the northern Great Barrier Reef where it is the dominant species of most outer reef slopes, Usually less dominant elsewhere in Australia and most other countries.
Acropora pharaonis	Common	0.55	Common	Common	Common
Acropora pinguis	Uncommon	0.1	NA	Uncommon	Common in the central Indian Ocean, uncommon elsewhere.
Acropora plantaginea	Common	0.55	NA	Common	Common
Acropora polystoma	Uncommon	0.1	Uncommon	Uncommon	Uncommon
Acropora pulchra	Uncommon	0.1	Uncommon	Uncommon	Usually uncommon but may be a dominant species
Acropora retusa	Uncommon	0.1	Uncommon	Uncommon	Common in South Africa, uncommon elsewhere
Acropora robusta	Common	0.55	Common	Not Clear	Common in the central Indo-Pacific
Acropora rosaria	Sometimes common	0.3	NA	Sometimes common	Sometimes common
Acropora roseni	Uncommon	0.1	Uncommon	Uncommon	Uncommon
Acropora samoensis	Uncommon	0.1	Common	Uncommon	Usually uncommon
Acropora secale	Uncommon	0.1	Common	Uncommon	Common in the Pacific, uncommon in the Indian Ocean
Acropora squarrosa	Common	0.55	Common	Common	Common

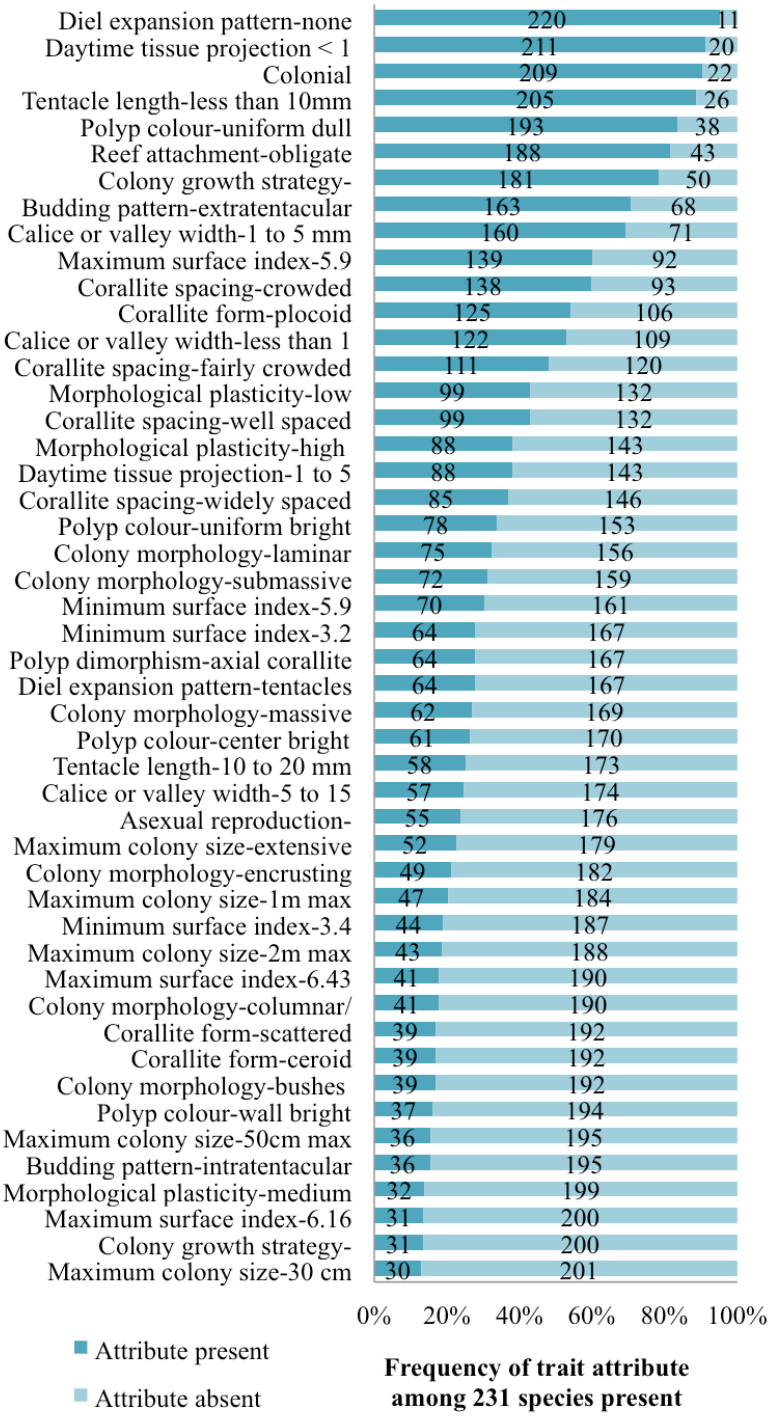
Species	Commonality used for weighting	Weighting	Commonality based on Carpenter et al. 2009	Commonality based on Veron 2000	Commonality Veron 2000 verbatum
Acropora striata	Rare	0.05	Rare	Rare	May be locally dominant in Japan, rare elsewhere
Acropora tenuis	Uncommon	0.1	Uncommon	Uncommon	Common in the western Pacific and Red Sea, uncommon elsewhere
Acropora valida	Sometimes Common	0.3	Common	Sometimes common	Sometimes common
Acropora variabilis	Uncommon	0.1	NA	Uncommon	Uncommon
Acropora variolosa	Uncommon	0.1	Uncommon	Uncommon	Uncommon
Acropora vermiculata	Common	0.55	NA	Common	Common, especially in the western Indian Ocean
Acropora verweyi	Common	0.55	Common	Common	Common, especially in the Western Indian Ocean
Acropora willisae	Rare	0.05	Uncommon	Rare	Common in Western Australia, rare elsewhere
Acropora yongei	Common	0.55	Common	Common	Common
Cycloseris costulata	Rare	0.05	NA	Rare	Rare
Cycloseris curvata	Uncommon	0.1	NA	Uncommon	Uncommon
Cycloseris cyclolites	Common	0.55	NA	Common	Common
Cycloseris erosa	Rare	0.05	NA	Rare	Rare
Cycloseris patelliformis	Usually uncommon	0.1	NA	Usually uncommon	Usually uncommon
Cycloseris somervillei	Usually uncommon	0.1	NA	Usually uncommon	Usually uncommon
Cycloseris tenuis	Rare	0.05	NA	Rare	Rare
Cycloseris vaughani	Rare	0.05	NA	Rare	Rare
Fungia concinna	Common	0.55	Common	Common	Common

Species	Commonality used for weighting	Weighting	Commonality based on Carpenter et al. 2009	Commonality based on Veron 2000	Commonality Veron 2000 verbatum
Fungia corona	Common	0.55	NA	Common	Common in the Red Sea and western Indian Ocean, uncommon elsewhere.
Fungia danai	Common	0.55	NA	Common	Common
Fungia fungites	Common	0.55	Common	Common	Common
Fungia horrida	Common	0.55	Common	Common	Common
Fungia klunzingeri	Common	0.55	NA	Common	Common in the western Indian Ocean and Red Sea, uncommon elsewhere
Fungia paumotensis	Common	0.55	Common	Common	Common
Fungia repanda	Common	0.55	Common	Common	Common
Fungia scruposa	Uncommon	0.1	Common	Uncommon	Uncommon
Fungia scutaria	Common	0.55	Common	Common	Common and distinctive
Fungia seychellensis	Uncommon	0.1	Common	Uncommon	Uncommon
Montipora aequituberculata	Common	0.55	Common	Common	Common; may be a dominant species on sheltered upper reef slopes
Montipora australiensis	Rare	0.05	Rare	Rare	Rare
Montipora calcarea	Rare	0.05	Uncommon	Rare	Rare
Montipora danae	Common	0.55	Common	Common	Common
Montipora digitata	Common	0.55	Common	Common	Common
Montipora efflorescens	Common	0.55	Uncommon	Common	Common
Montipora effusa	Uncommon	0.1	Uncommon	Uncommon	Uncommon
Montipora floweri	Rare	0.05	Uncommon	Rare	Common in the Coral Sea, rare and inconspicuous elsewhere
Montipora foliosa	Common	0.55	Common	Common	Common
Montipora friabilis	Usually uncommon	0.1	Uncommon	Usually uncommon	Usually uncommon

Species	Commonality used for weighting	Weighting	Commonality based on Carpenter et al. 2009	Commonality based on Veron 2000	Commonality Veron 2000 verbatum
Montipora grisea	Common	0.55	Common	Common	Common
Montipora hispida	Common	0.55	Common	Uncommon	Common on the Great Barier Reef, usually uncommon elsewhere
Montipora informis	Common	0.55	Common	Common	Common
Montipora kellyi	Common	0.55	NA	Common	Common
Montipora lobulata	Rare	0.05	Rare	Rare	Rare
Montipora millepora	Common	0.55	Common	Common	Common but inconspicuous
Montipora mollis	Common	0.55	Common	Common	Especially common in high latitude location of Australia
Montipora monasteriata	Common	0.55	Common	Common	Common
Montipora orientalis	Rare	0.05	Rare	Rare	Rare
Montipora peltiformis	Uncommon	0.1	Uncommon	Uncommon	Uncommon
Montipora spongodes	Uncommon	0.1	Common	Uncommon	Uncommon
Montipora spumosa	Common	0.55	Common	Common	Common
Montipora tuberculosa	Common	0.55	Common	Common	Common
Montipora turgescens	Common	0.55	Common	Common	Common
Montipora undata	Common	0.55	Uncommon	Common	Common
Montipora venosa	Uncommon	0.1	Uncommon	Uncommon	Uncommon
Montipora verrucosa	Sometimes common	0.3	Uncommon	Sometimes common	Sometimes common
Porites lobata	Common	0.55	Common	Common	Probably the most common Porites
Porites lutea	Common	0.55	Common	Common	Common
Porites solida	Common	0.55	Common	Common	Common

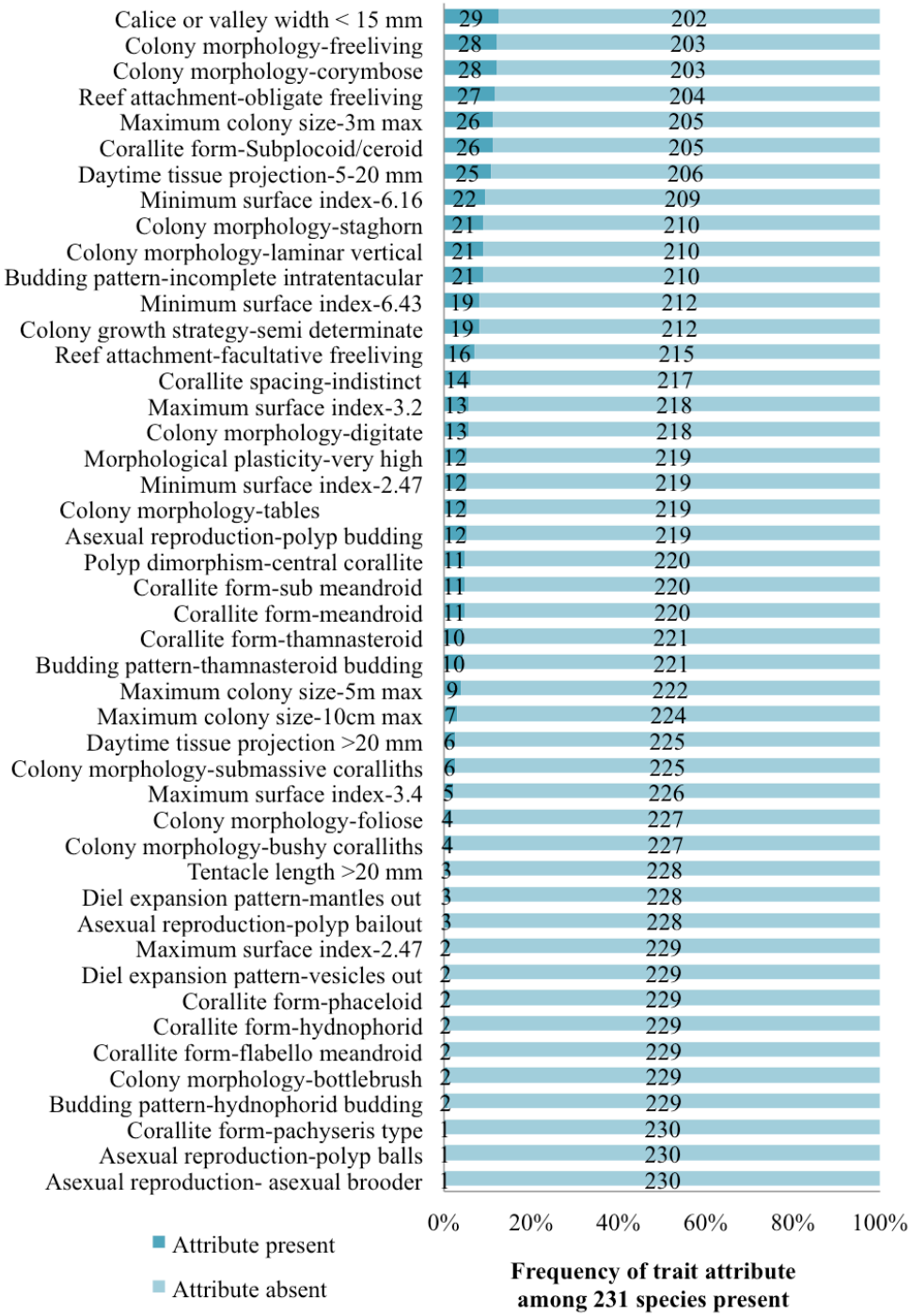
6. Trait rarity

6.1. Attribute frequency



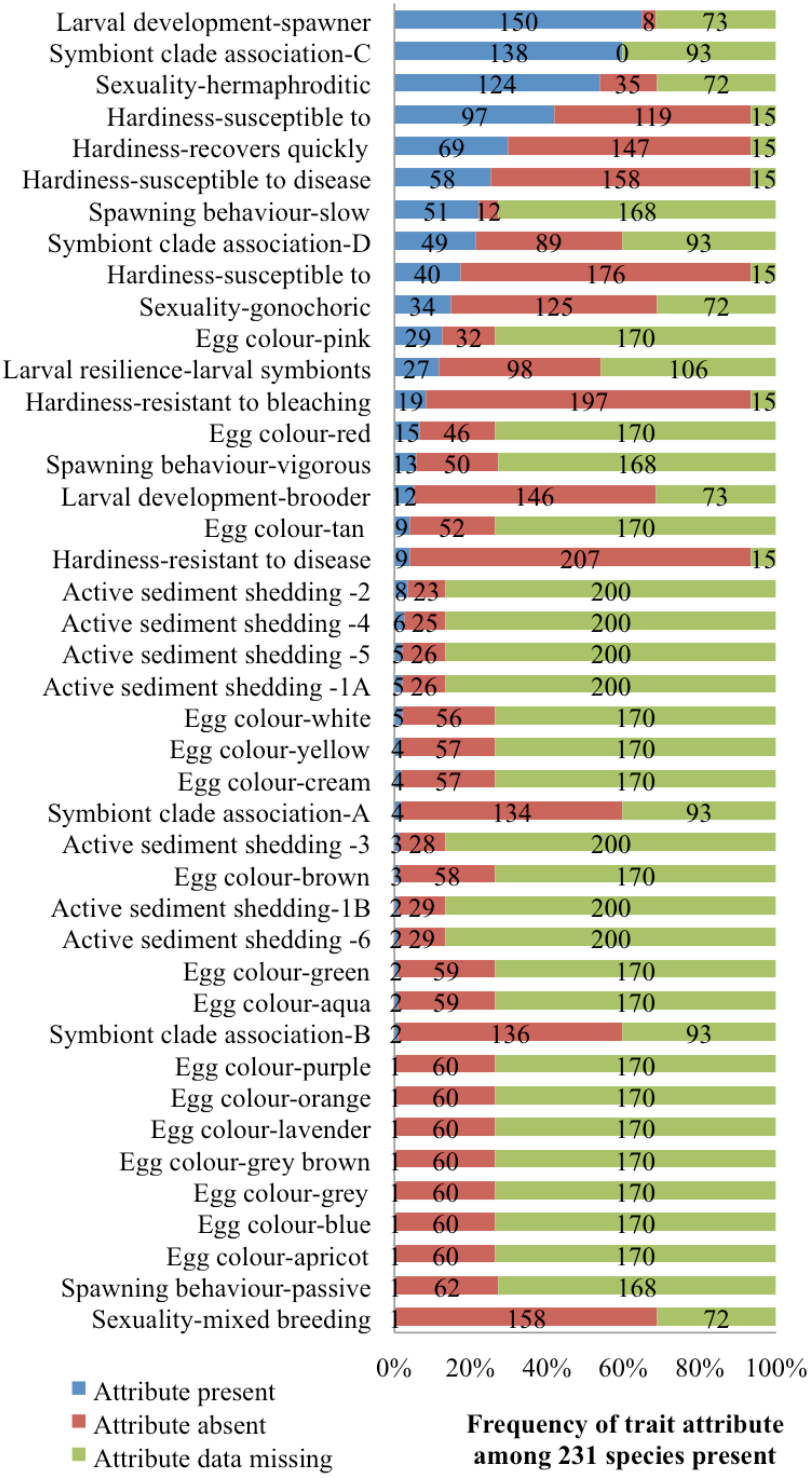
Frequency of attributes for traits with data available for all 231 species considered in this study.

6.1 cont. Attribute frequency



Frequency of attributes for traits with data available for all 231 species considered in this study.

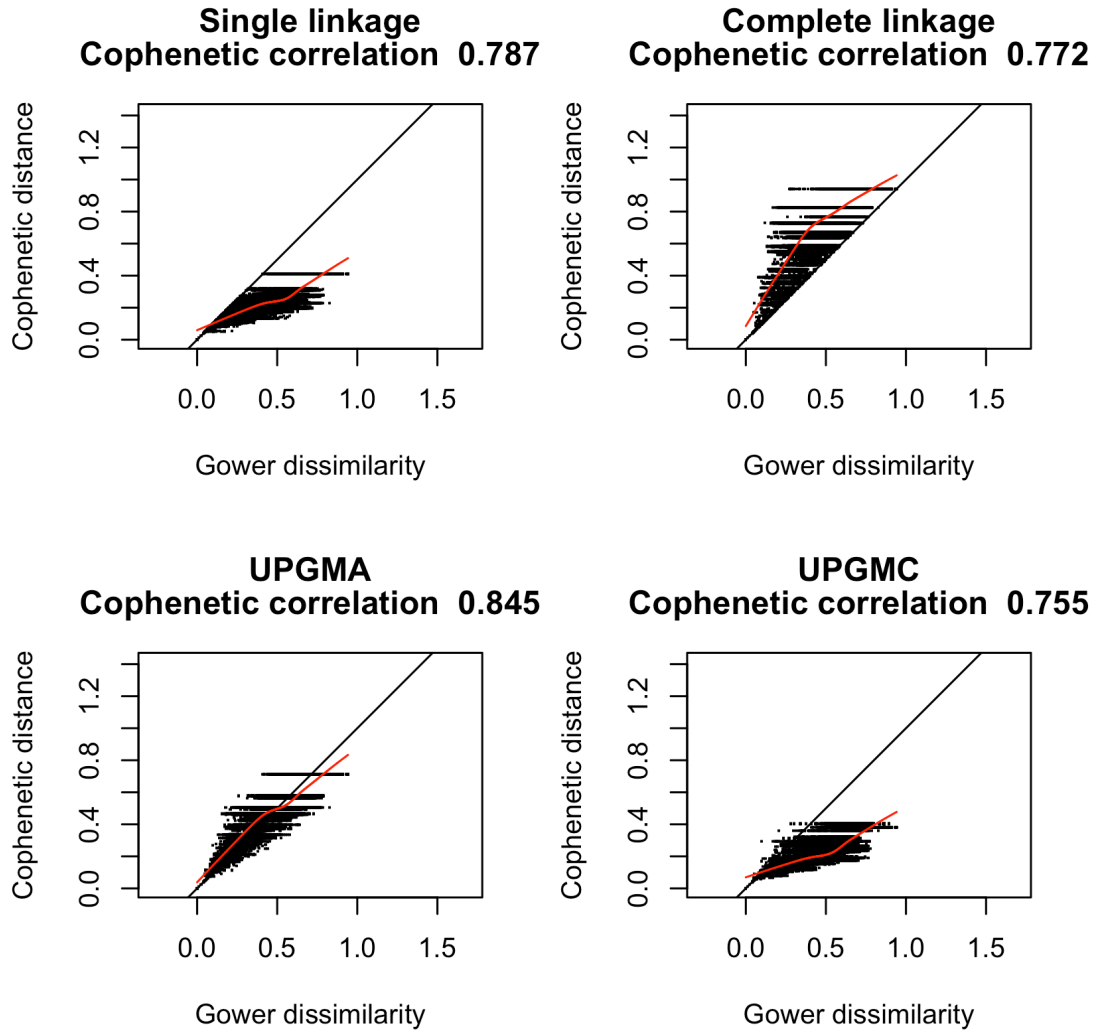
6.2. Attribute frequency for traits with missing data



Frequency of attributes for the 8 traits for which data is not available for all 231 species considered in this study.

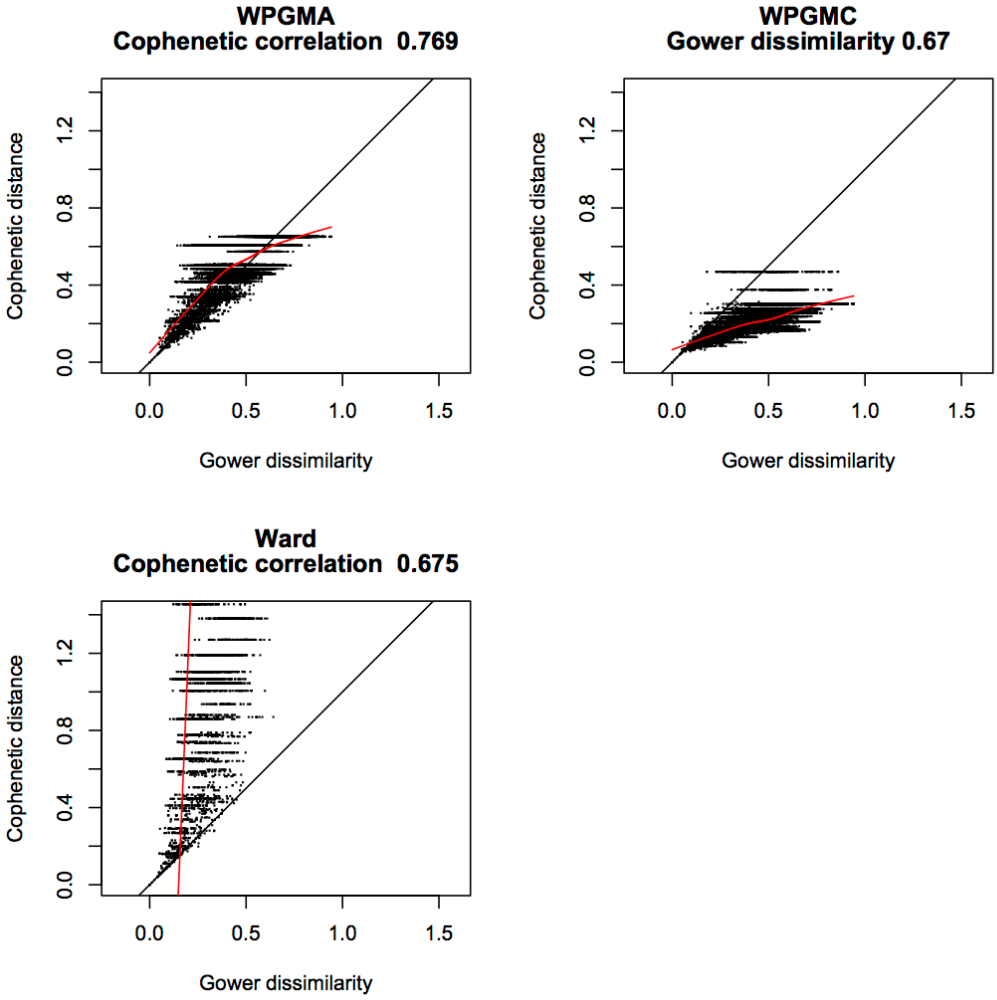
7. Species clustering Quality Control

7.1. Cophenetic correlation (W2 weighting)



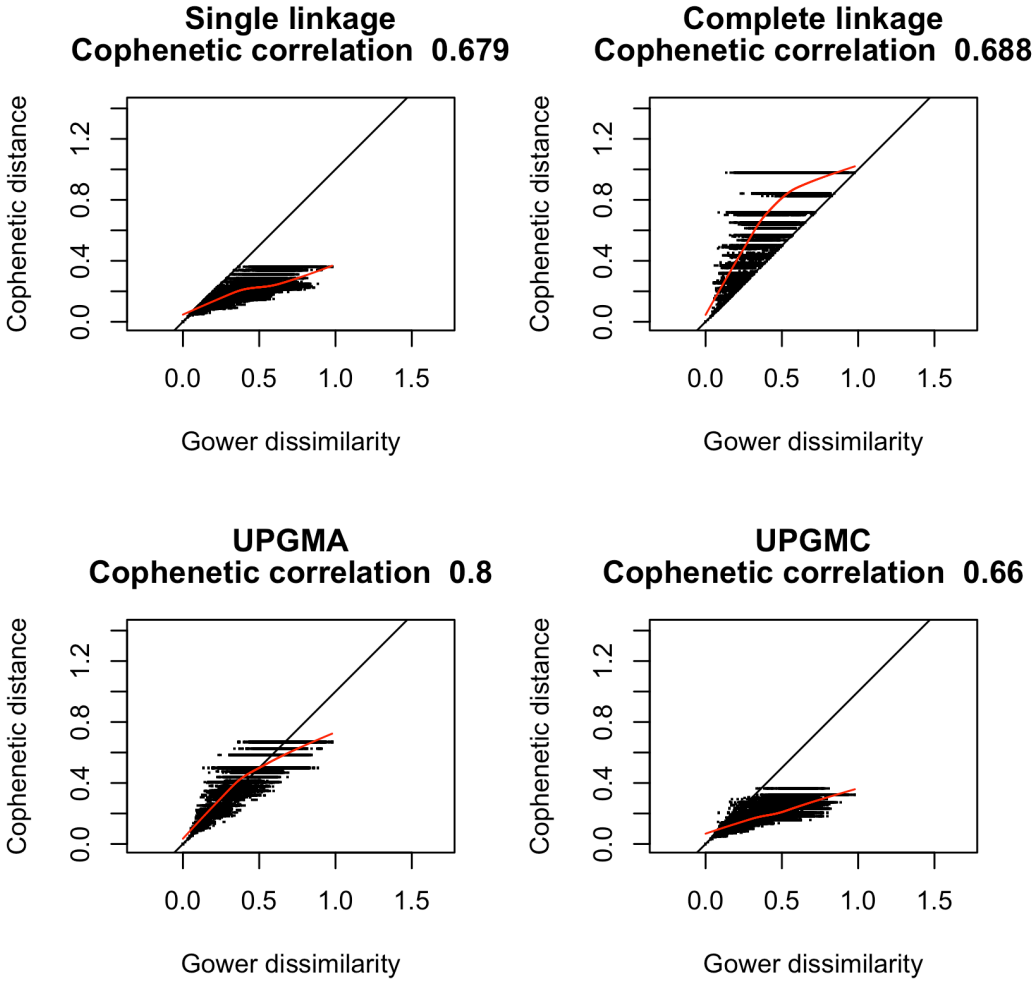
Cophenetic correlations between the W2 gower dissimilarity matrix and the cophenetic distance matrix testing how well clustering methods represent the original Gower species-species distance matrix. A LOWESS smoother shows the trend in each plot. The clustering methods tested here are: single linkage agglomerative clustering, complete linkage agglomerative clustering, unweighted pair-group method using arithmetic average (UPGMA) and unweighted pair-group method using centroids (UPGMC). A higher correlation value indicates the clustering model is better at representing the original distance matrix. This type of correlation cannot be tested for significance and simply a tool for selecting the most appropriate clustering method.

Cophenetic correlation (W2 weighting cont.)



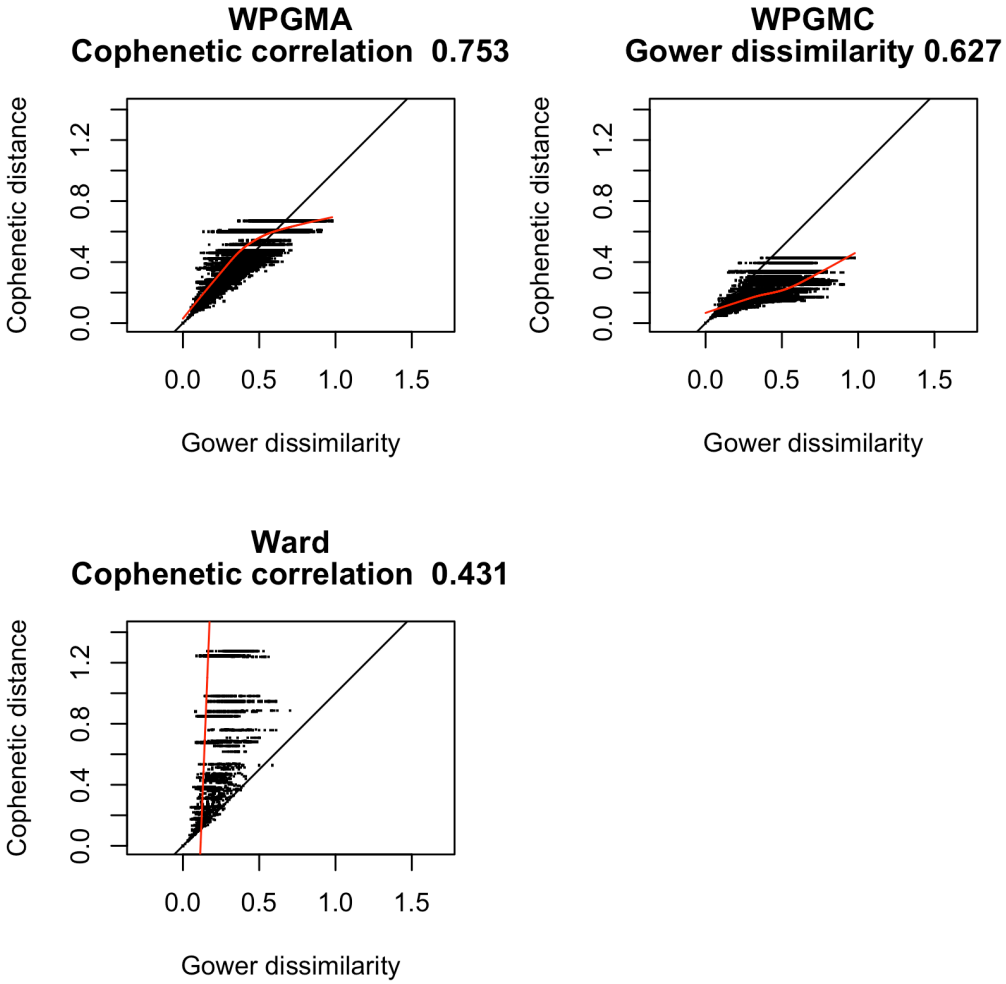
Cophenetic correlations between the W2 gower dissimilarity matrix and the cophenetic distance matrix testing how well clustering methods represent the original Gower species-species distance matrix. A LOWESS smoother shows the trend in each plot. The clustering methods tested here are: Weighted pair-group method using arithmetic averages (WPGMA), weighted pair-group method using centroids (WPGMC) and Ward's minimum variance clustering. A higher correlation value indicates the clustering model is better at representing the original distance matrix. This type of correlation cannot be tested for significance and simply a tool for selecting the most appropriate clustering method.

7.2. Cophenetic correlation (W3 weighting)



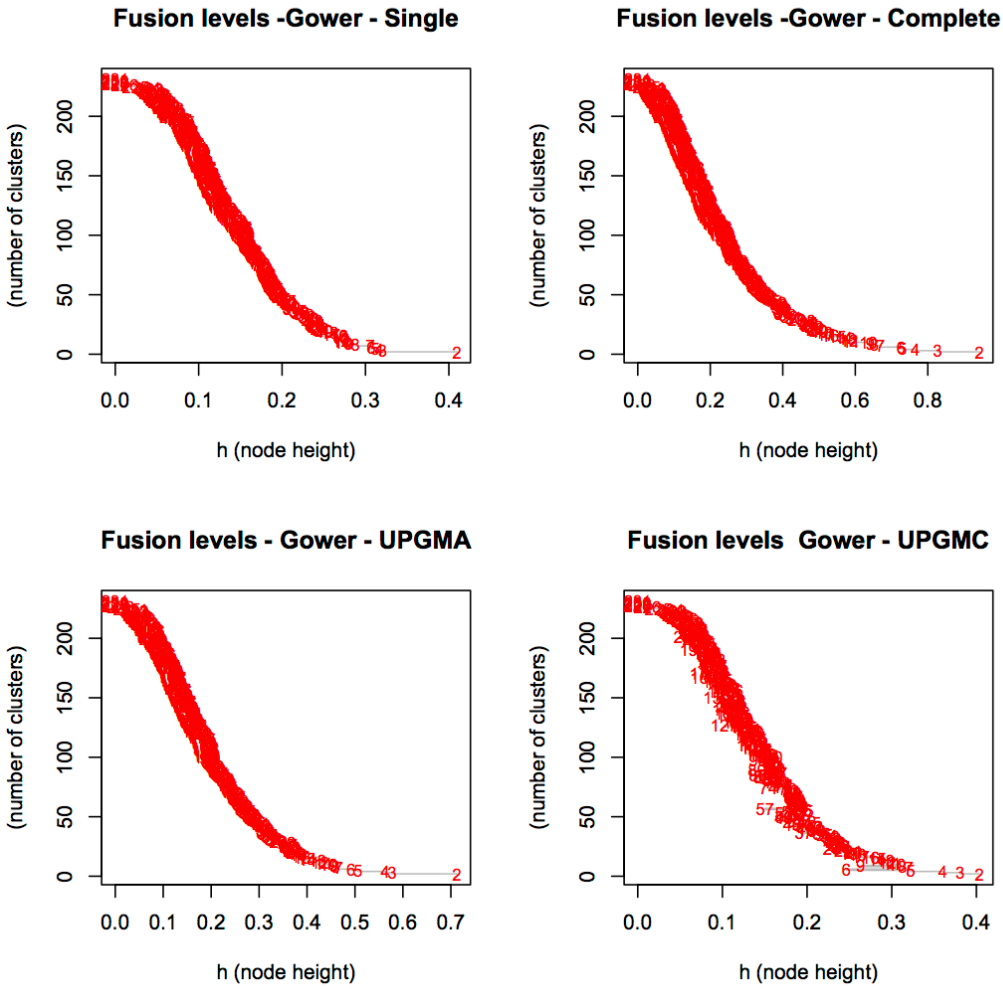
Cophenetic correlations between the W3 gower dissimilarity matrix and the cophenetic distance matrix testing how well clustering methods represent the original Gower species-species distance matrix. A LOWESS smoother shows the trend in each plot. The clustering methods tested here are: single linkage agglomerative clustering, complete linkage agglomerative clustering, unweighted pair-group method using arithmetic average (UPGMA) and unweighted pair-group method using centroids (UPGMC). A higher correlation value indicates the clustering model is better at representing the original distance matrix. This type of correlation cannot be tested for significance and simply a tool for selecting the most appropriate clustering method.

Cophenetic correlation (W3 weighting cont.)



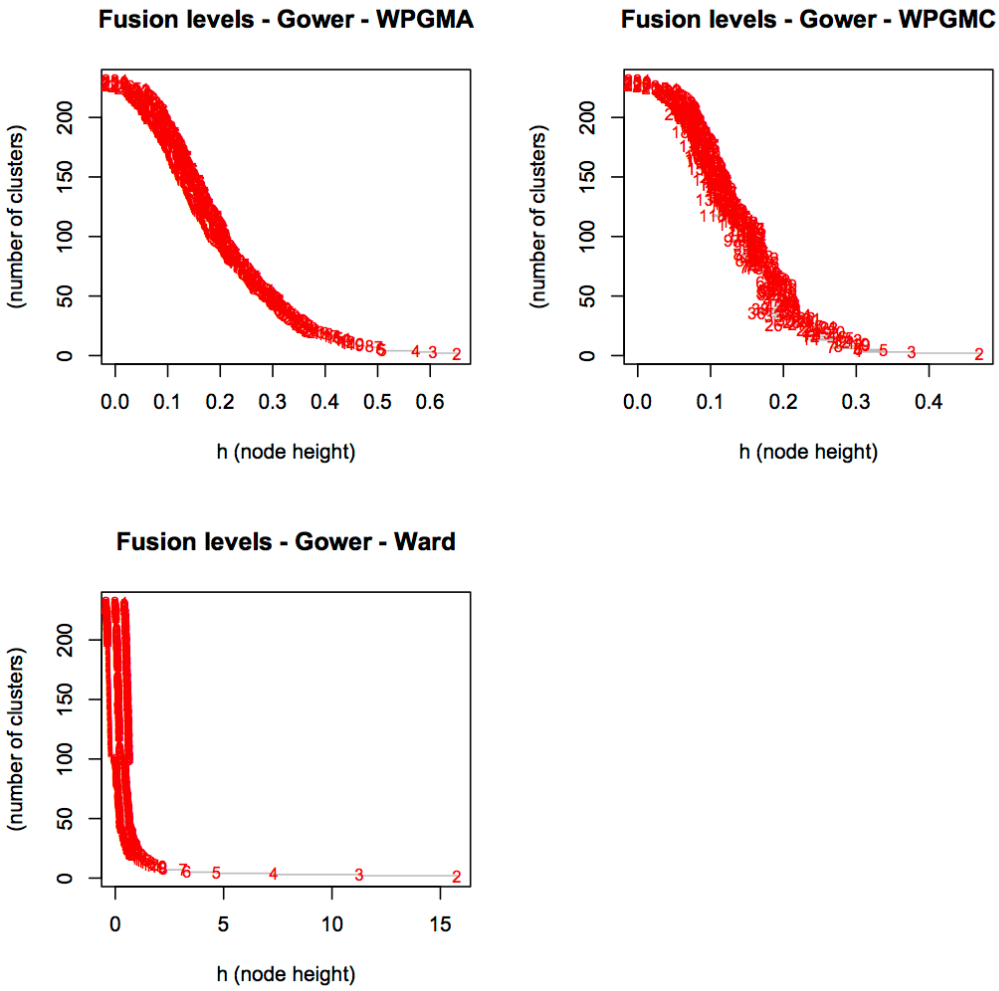
Cophenetic correlations between the W3 gower dissimilarity matrix and the cophenetic distance matrix testing how well clustering methods represent the original Gower species-species distance matrix. A LOWESS smoother shows the trend in each plot. The clustering methods tested here are: Weighted pair-group method using arithmetic averages (WPGMA), weighted pair-group method using centroids (WPGMC) and Ward's minimum variance clustering. A higher correlation value indicates the clustering model is better at representing the original distance matrix. This type of correlation cannot be tested for significance and simply a tool for selecting the most appropriate clustering method.

7.3. Fusion level plots (W2 weighting)



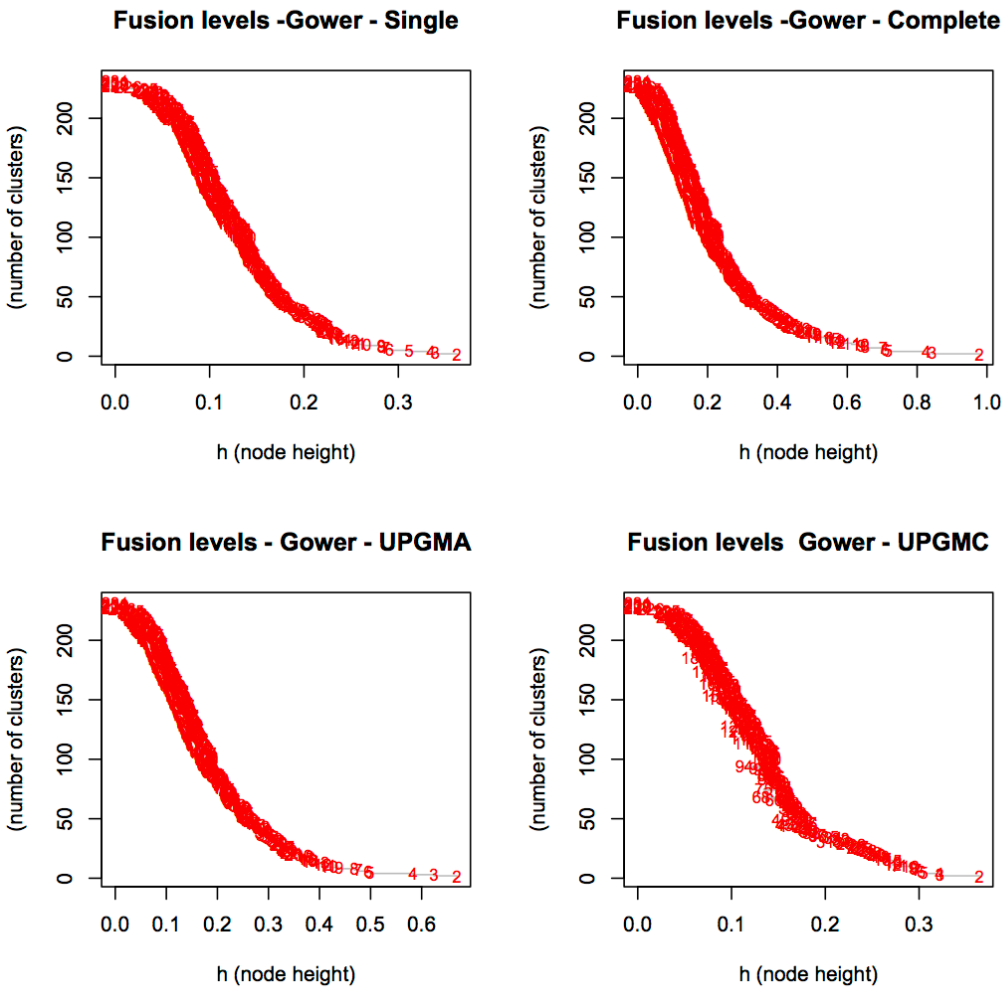
Plots of the levels of dissimilarity (node height) at which groups are fused. Fusion levels for single, complete, UPGMA and UPGMC clustering models on the W2 weighted Gower dissimilarity of the species trait matrix are shown. All possible numbers of clusters (i.e. all fusion in the entire dendrogram) is shown.

Fusion level plots (W2 weighting) cont.



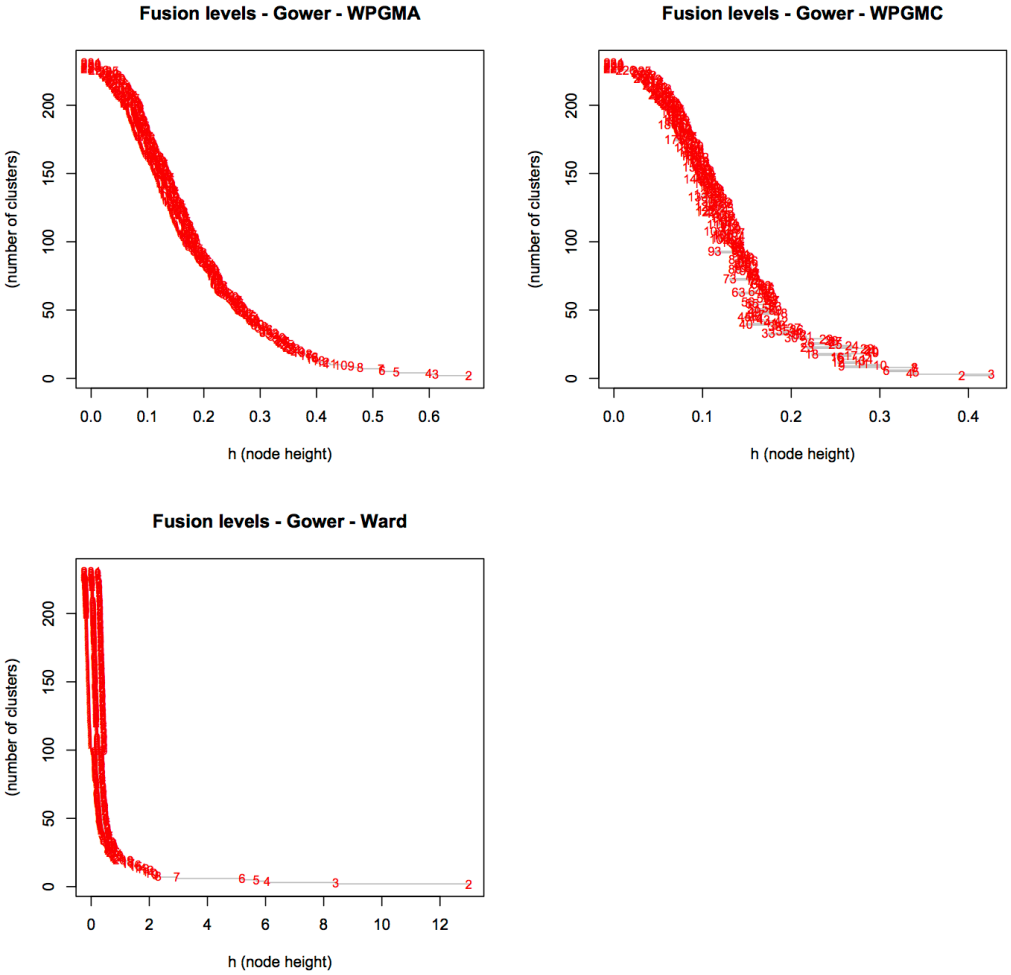
Plots of the levels of dissimilarity (node height) at which groups are fused. Fusion levels for WPGMA, WPGMC, and ward's clustering models on the W2 weighted Gower dissimilarity of the species trait matrix are shown. All possible numbers of clusters (i.e. all fusion in the entire dendrogram) is shown.

7.4. Fusion level plots (W3 weighting)



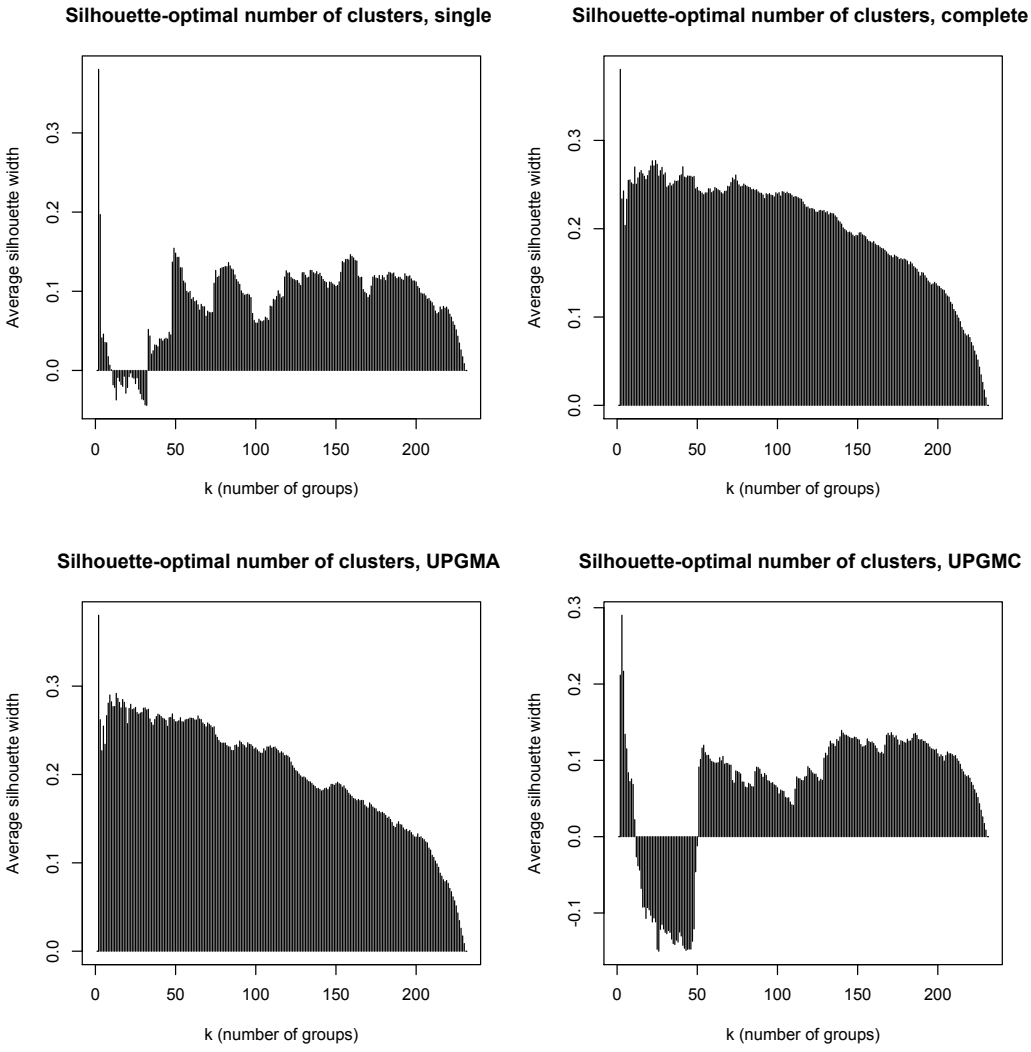
Plots of the levels of dissimilarity (node height) at which groups are fused. Fusion levels for single, complete, UPGMA and UPGMC clustering models on the W3 weighted Gower dissimilarity of the species trait matrix are shown. All possible numbers of clusters (i.e. all fusion in the entire dendrogram) is shown.

Fusion level plots (W3 weighting) cont.



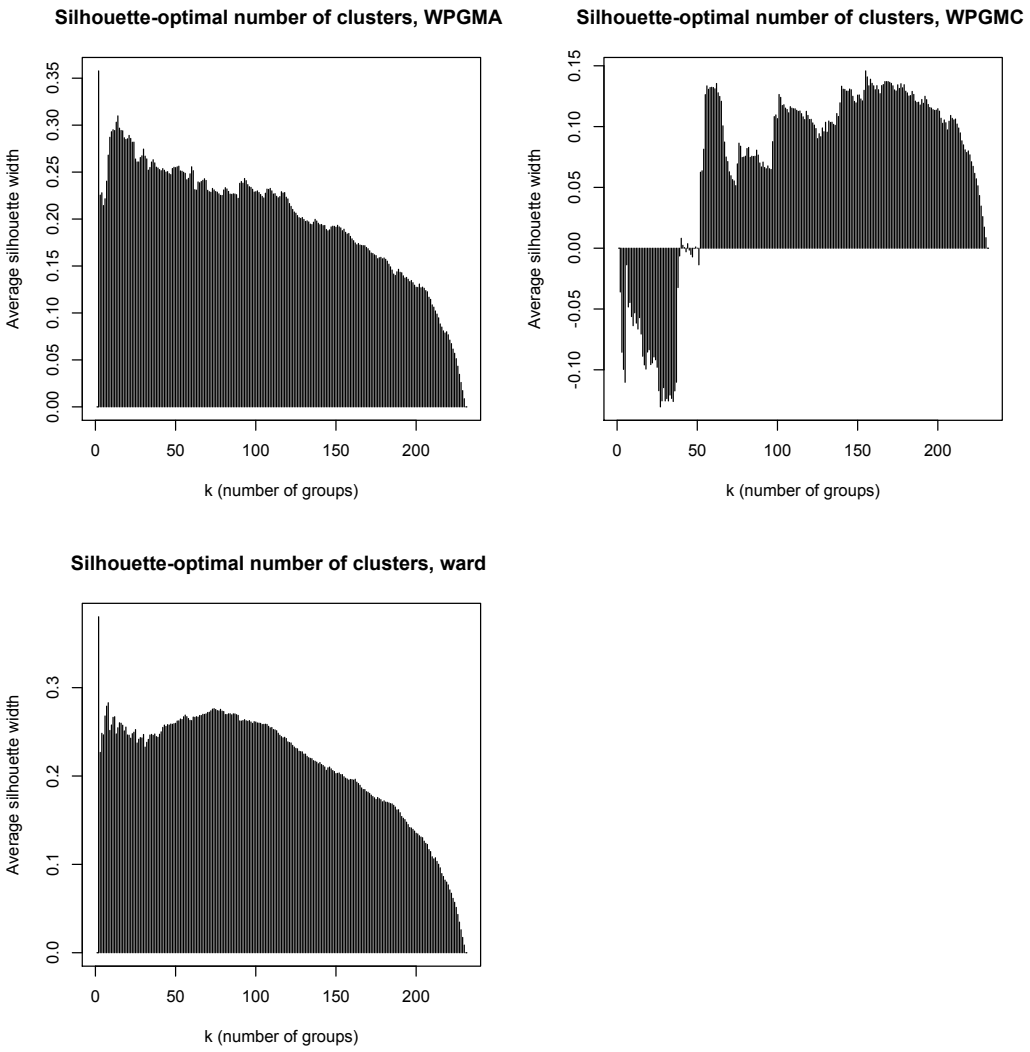
Plots of the levels of dissimilarity (node height) at which groups are fused. Fusion levels for WPGMA, WPGMC, and ward's clustering models on the W3 weighted Gower dissimilarity of the species trait matrix are shown. All possible numbers of clusters (i.e. all fusion in the entire dendrogram) is shown.

7.5. Silhouette graphs (W2 weighting)



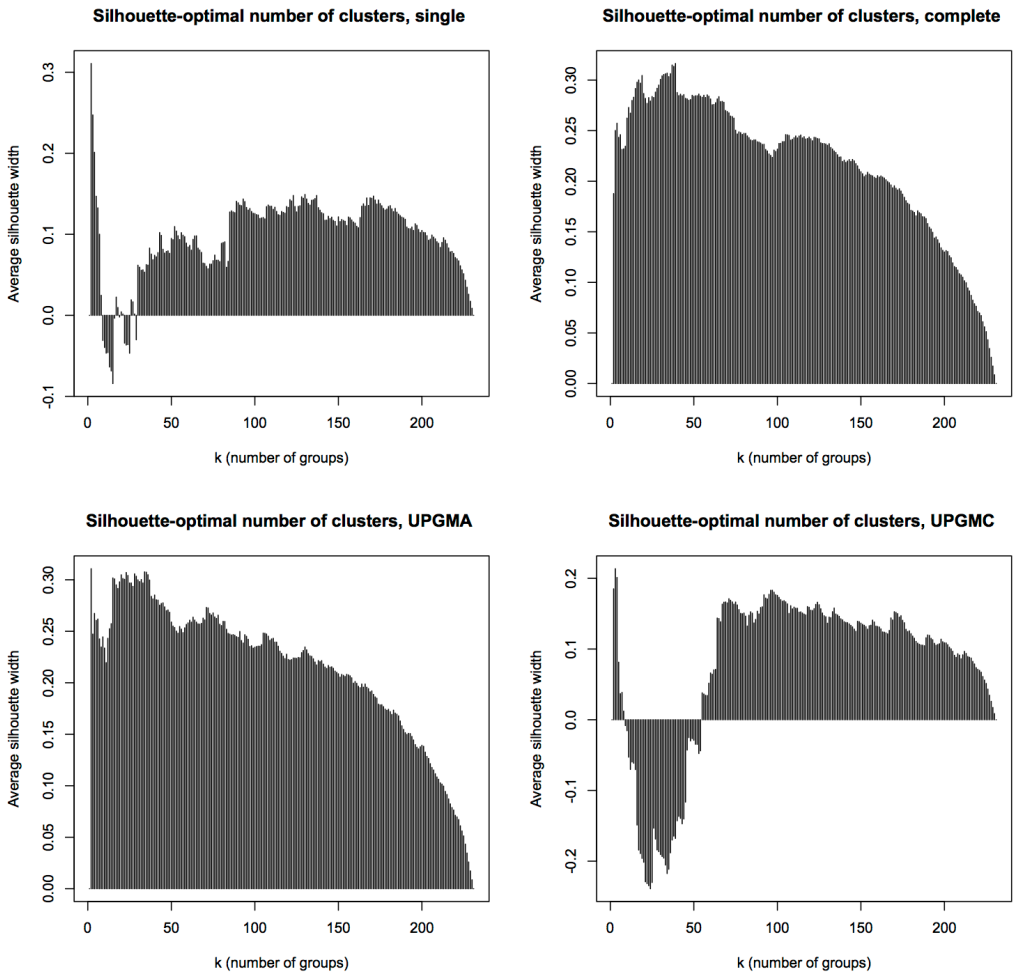
Silhouette graphs for the average silhouette width for cluster members at different levels along the dendrogram (k). The single, complete, UPGMA, and GPGMC clustering models of species in terms of the W2 weighted Gower dissimilarity of the species-trait matrix are shown. Greater widths show greater cluster coherence. Negative values indicated misplaced members.

Silhouette graphs (W2 weighting) cont.



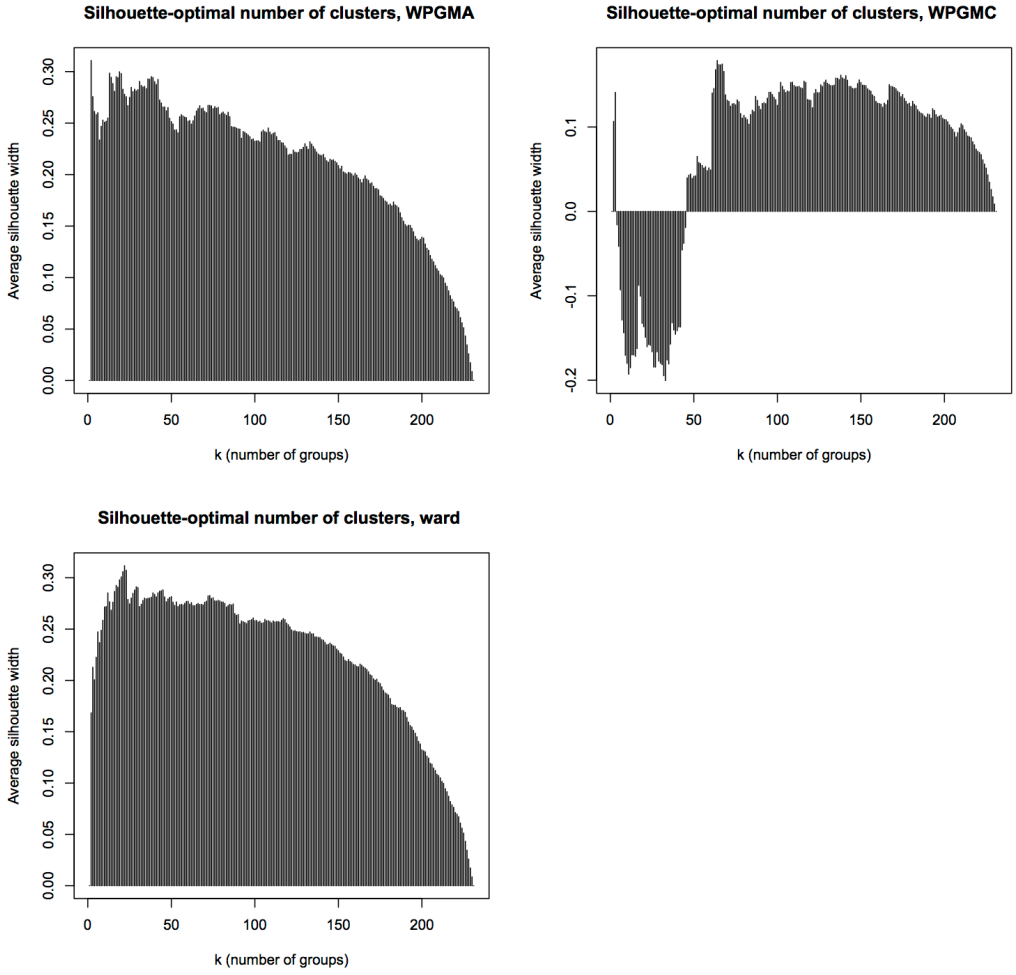
Silhouette graphs for the average silhouette width for cluster members at different levels along the dendrogram (k). The WPGMA, WPGMC, and ward's clustering models of species in terms of the W2 weighted Gower dissimilarity of the species-trait matrix are shown. Greater widths show greater cluster coherence. Negative values indicated misplaced members.

7.6. Silhouette graphs (W3 weighting)



Silhouette graphs for the average silhouette width for cluster members at different levels along the dendrogram (k). The single, complete, UPGMA, and GPGMC clustering models of species in terms of the W3 weighted Gower dissimilarity of the species-trait matrix are shown. Greater widths show greater cluster coherence. Negative values indicated misplaced members.

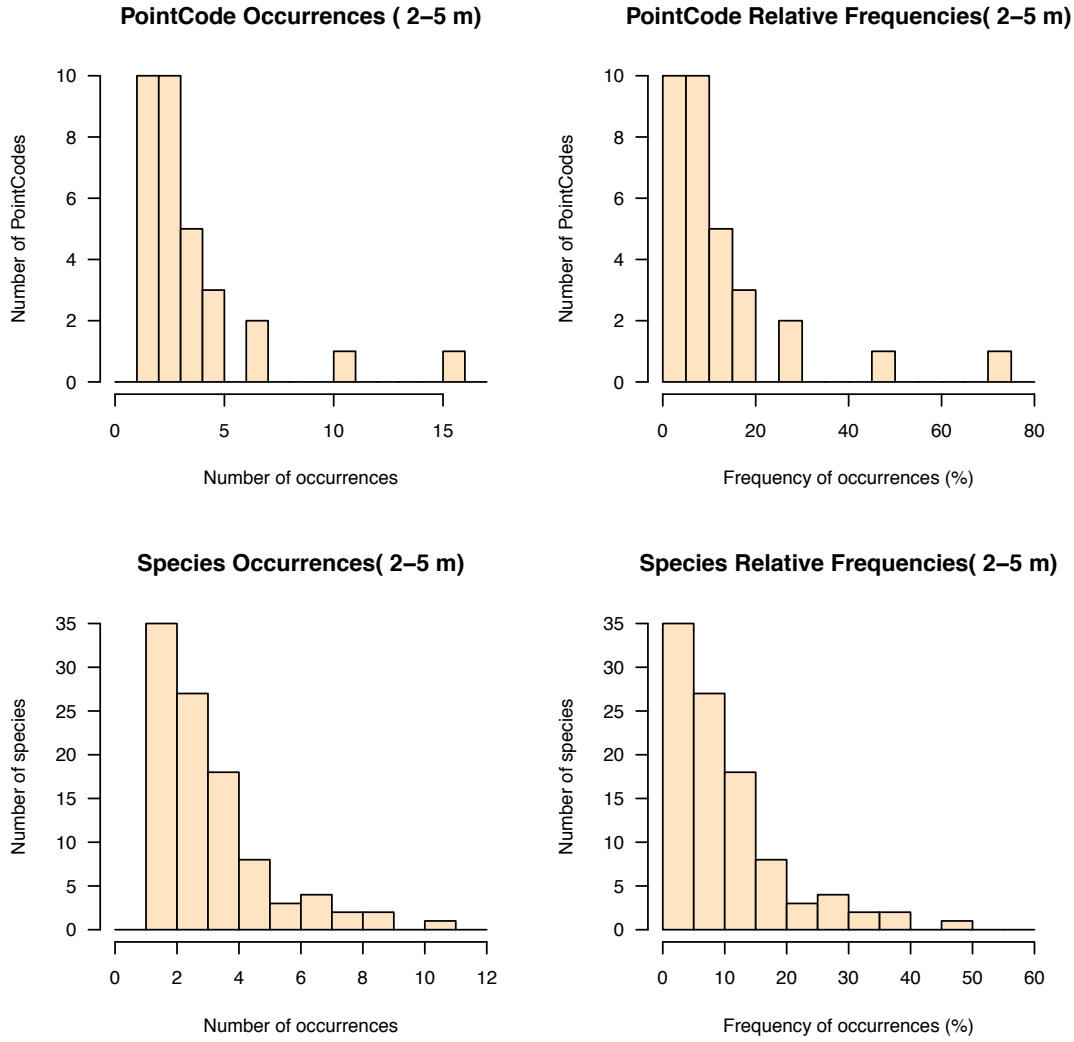
Silhouette graphs W3 weighting cont.



Silhouette graphs for the average silhouette width for cluster members at different levels along the dendrogram (k). The WPGMA, WPGMC, and ward's clustering models of species in terms of the W3 weightedGower dissimilarity of the species-trait matrix are shown. Greater widths show greater cluster coherence. Negative values indicated misplaced members.

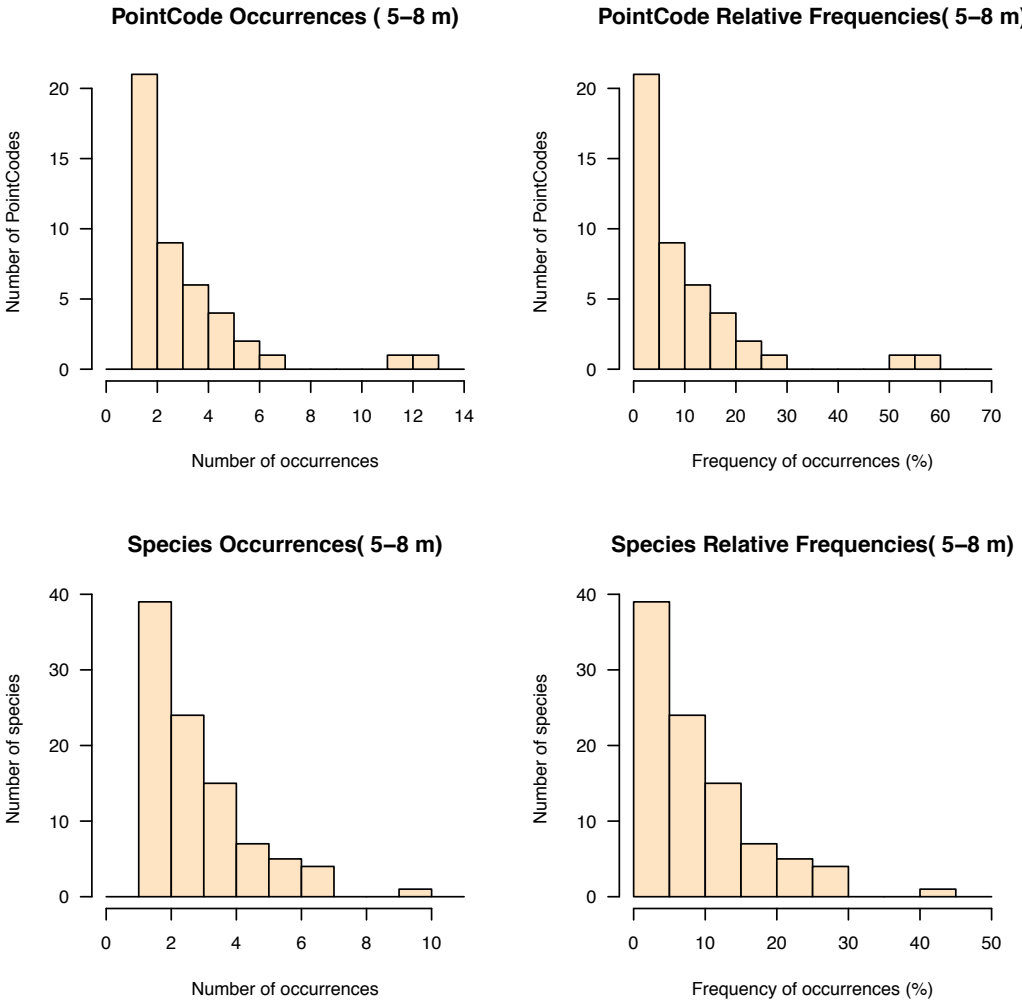
8. Species replacement quality control

8.1. 2-5 m depth



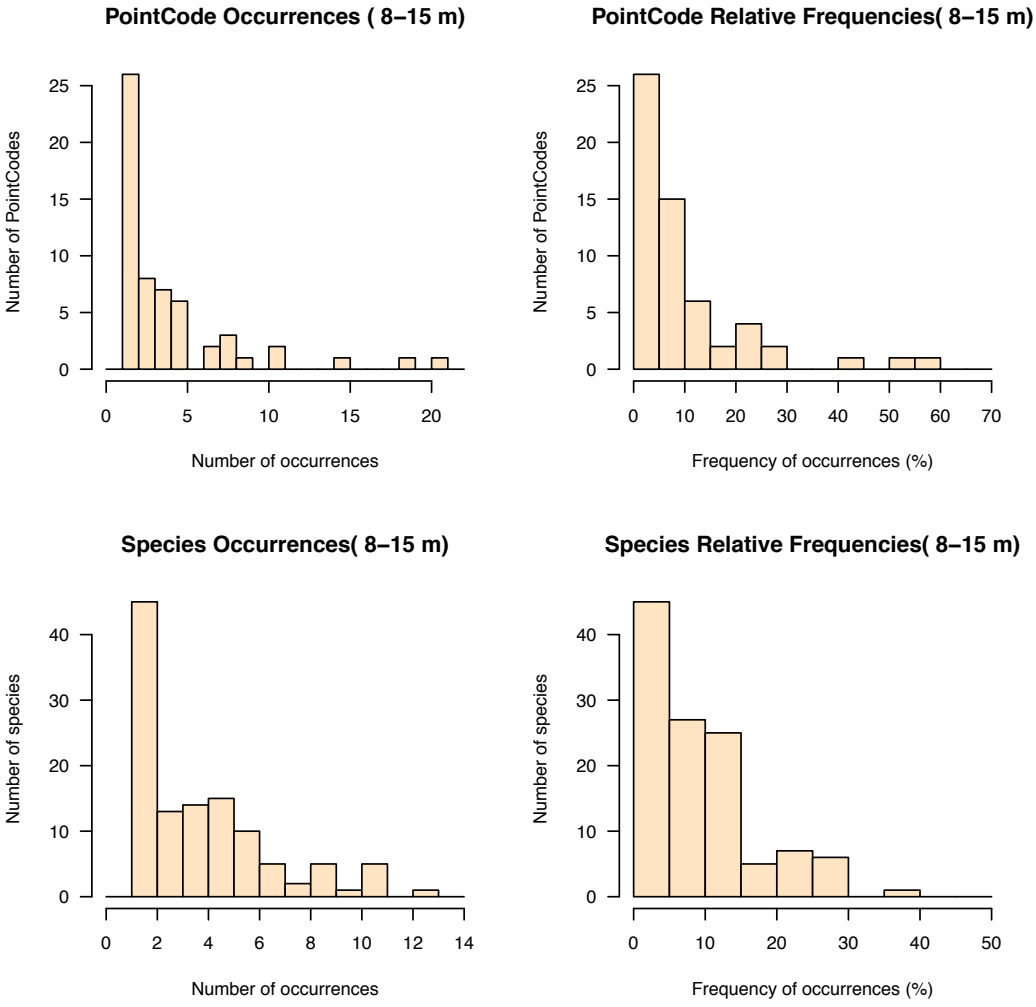
The influence of commonality weighted replacement of species clusters with actual species on frequency distribution for the two to five metre depth range.

8.2. 5-8 m depth



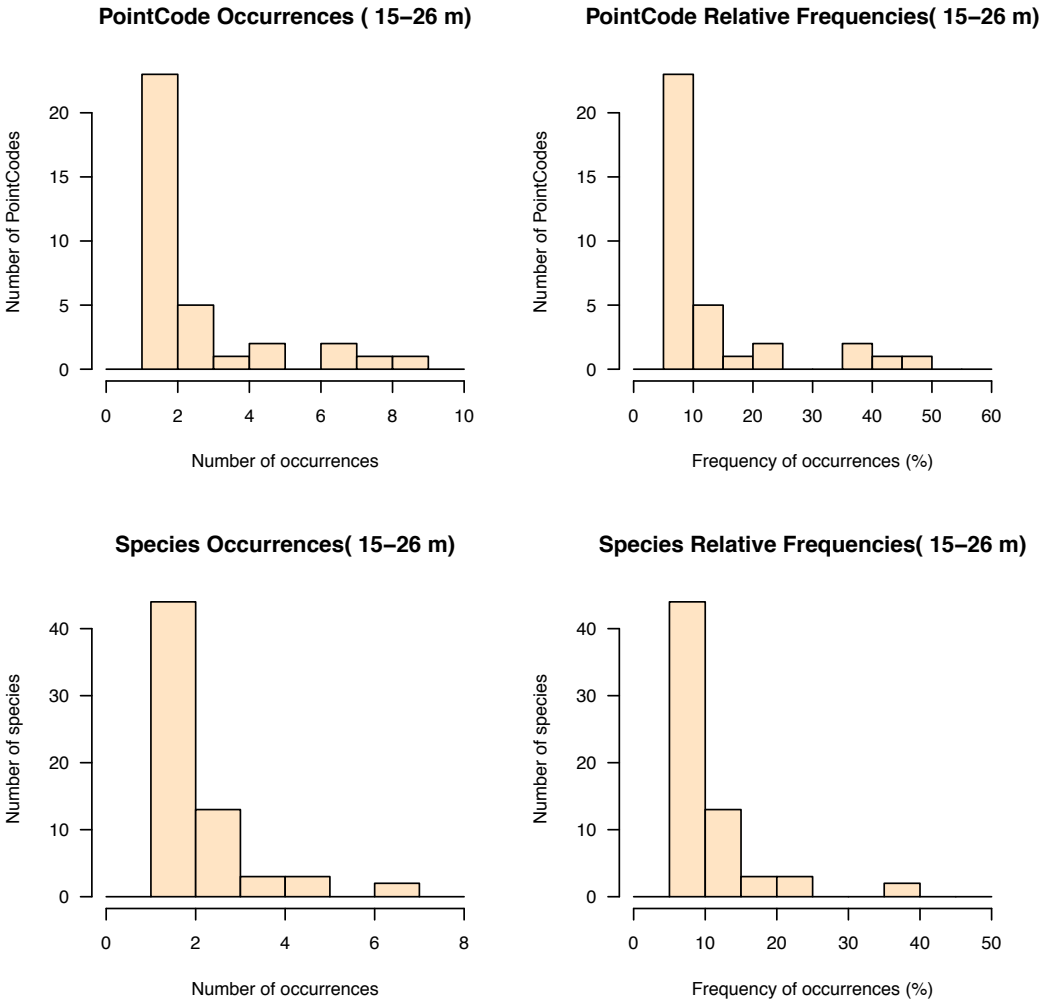
The influence of commonality weighted replacement of species clusters with actual species on frequency distribution for the five to eight metre depth range.

8.3. 8-15 m depth



The influence of commonality weighted replacement of species clusters with actual species on frequency distribution for the eight to 15 metre depth range.

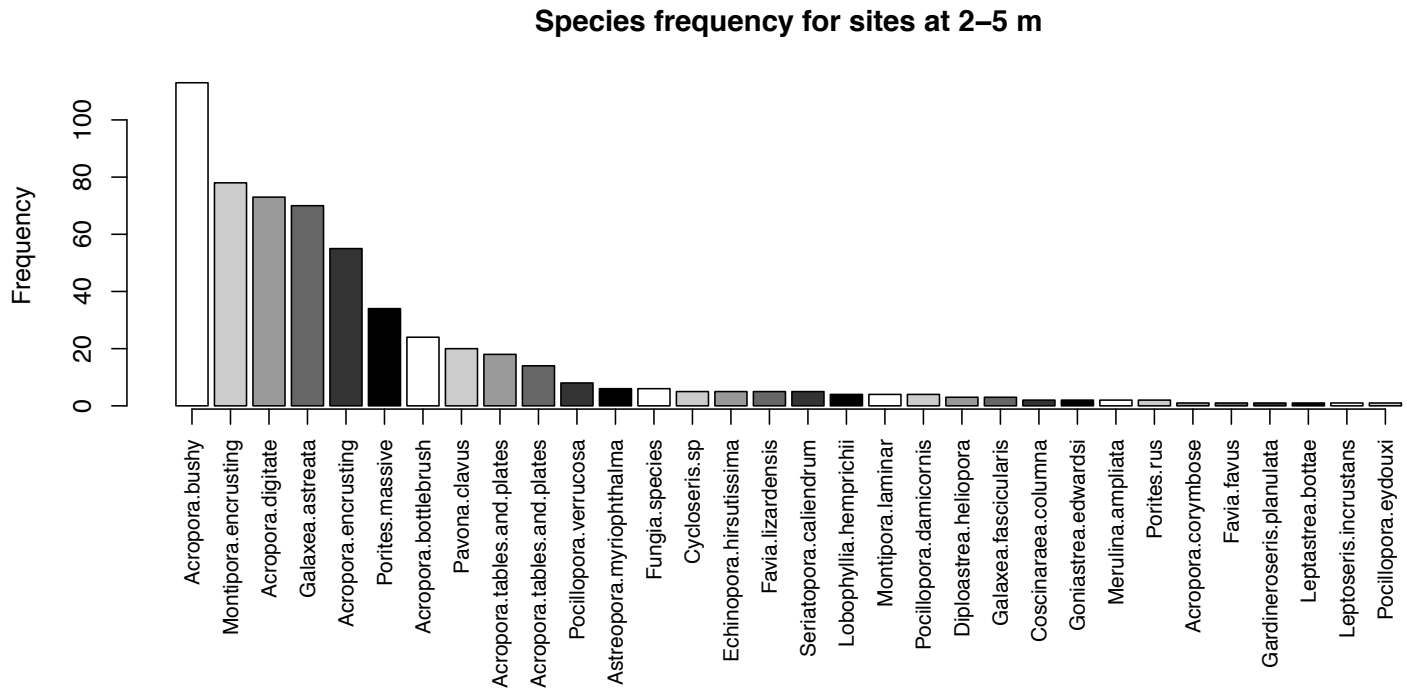
8.4. 15-26 m depth



The influence of commonality weighted replacement of species clusters with actual species on frequency distribution for the 15-26 m depth range.

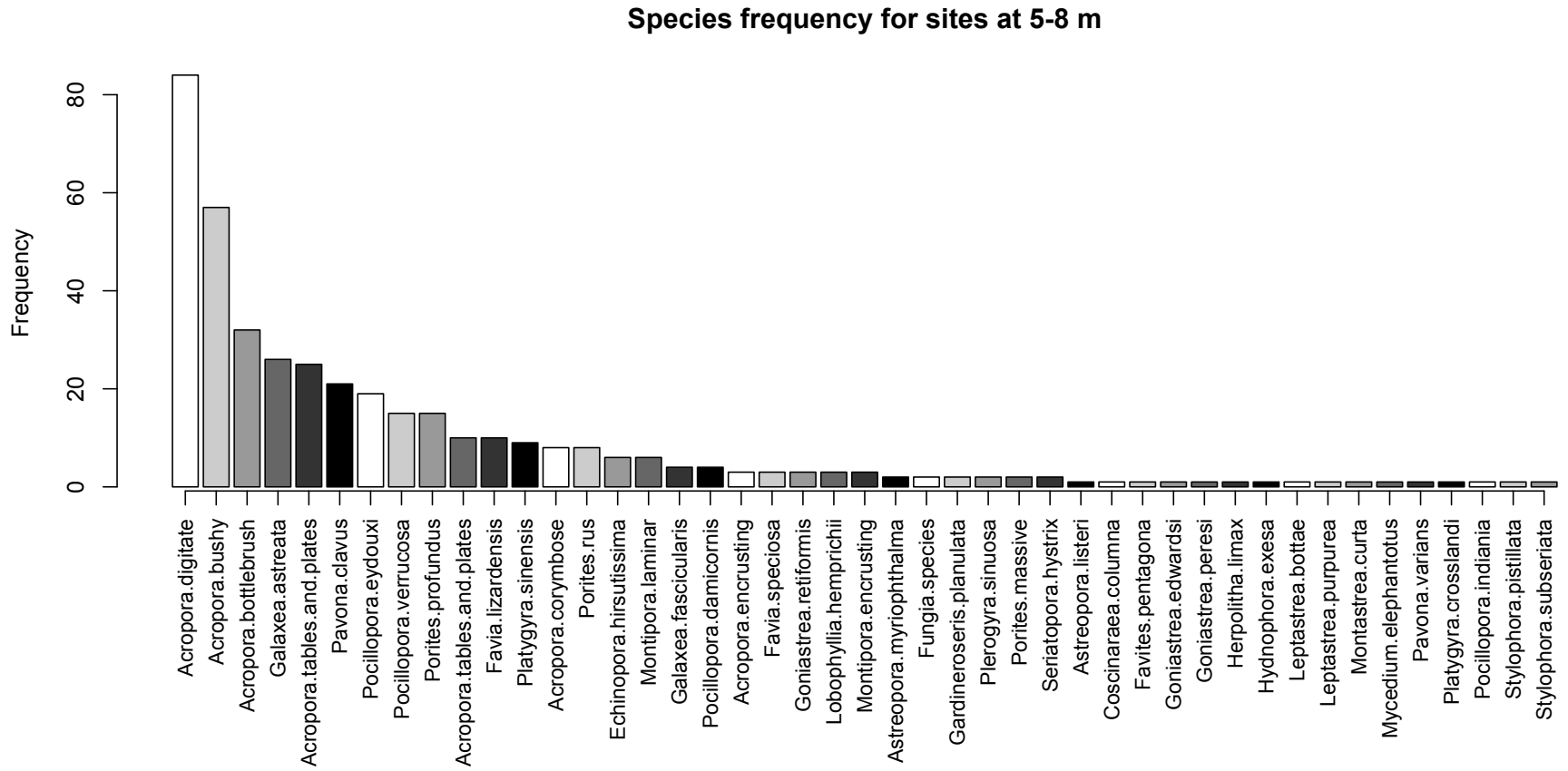
9. Species frequencies

9.1. 2-5 m depth



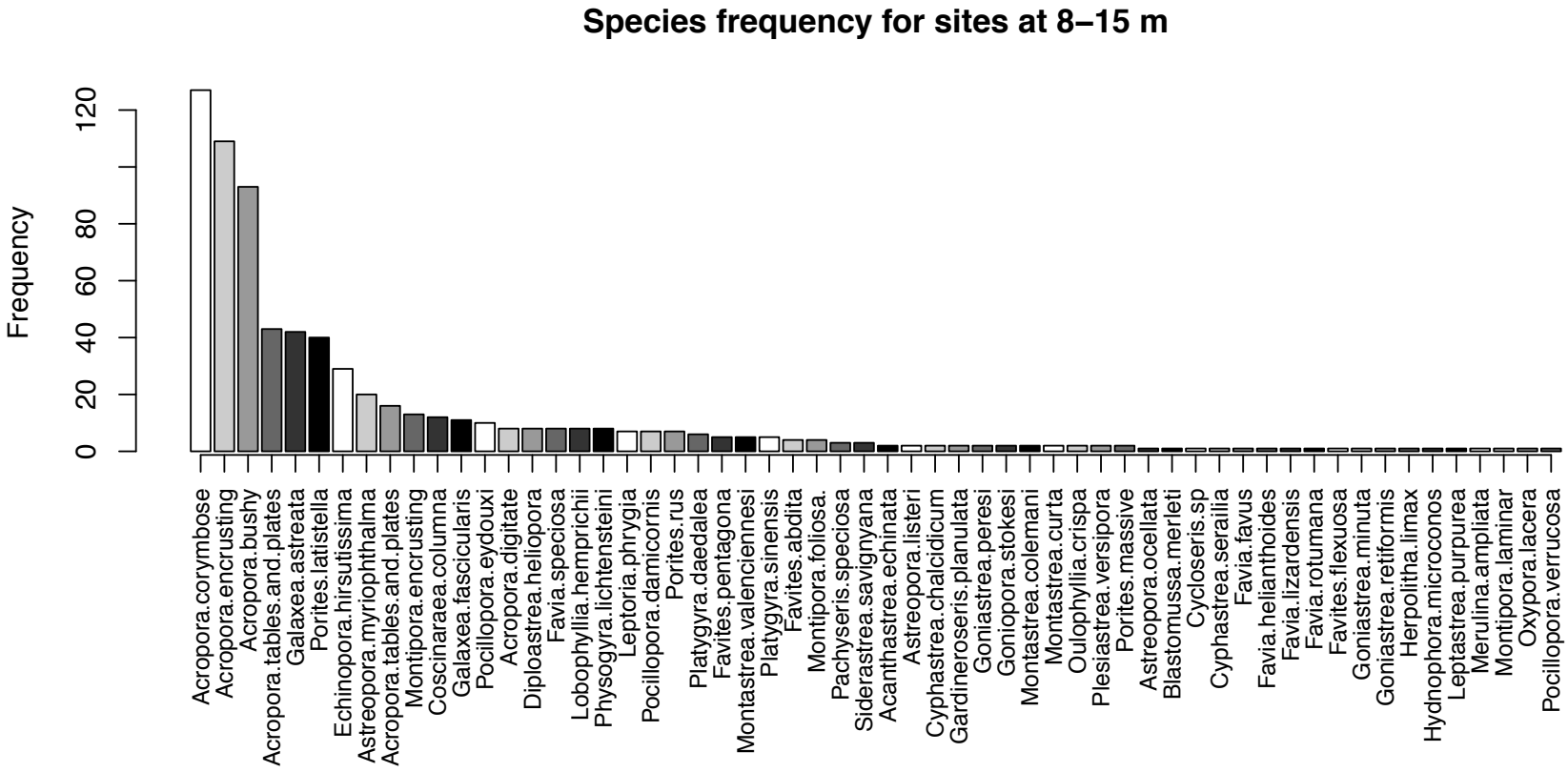
Species frequency distribution for the species and species clusters at two to five metres depth.

9.2. 5-8 m depth



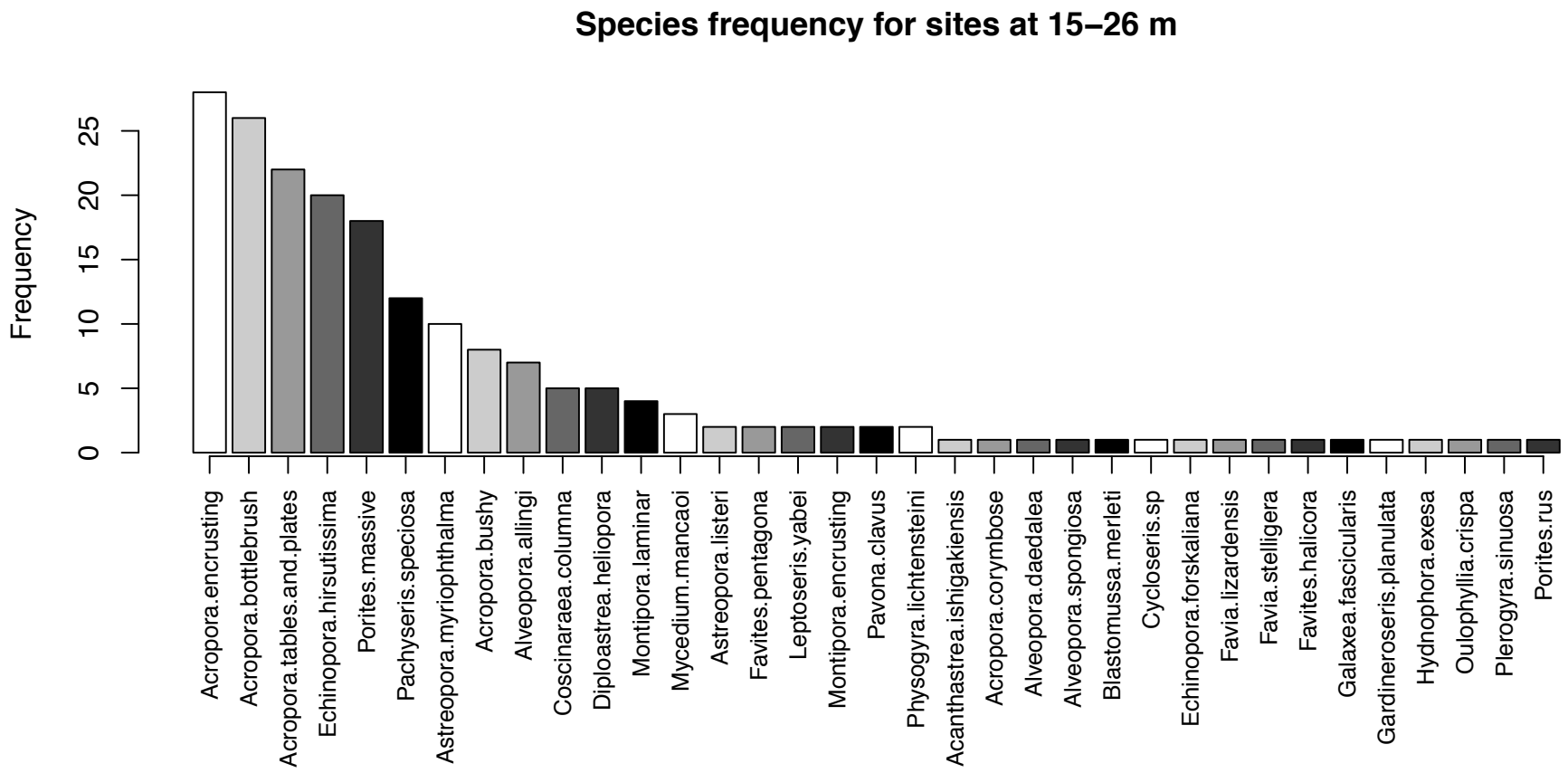
Species frequency distribution for the species and species clusters at five to eight metres depth.

9.3. 8-15 m depth



Species frequency distribution for the species and species clusters at eight to 15 metres depth.

9.4. 15-26 m depth



Species frequency distribution for the species and species clusters at 15-26 metres depth.

1. Digital Supplements

The following items are available in the attached CD as a digital supplement to this dissertation.

1.1. Trait data

1.1.1. Coral ID traits- All Species

The coral traits extracted from the electronic taxonomic key Coral ID (Veron and Stafford-Smith, 2002) for 795 coral species. Traits and attributes are separated by a dash. Trait attributes are coded as a binary matrix and are formatted for import into R.

1.1.2. Coral ID traits -Southwest Madagascar

The coral traits extracted from the electronic taxonomic key Coral ID (Veron and Stafford-Smith, 2002) for 231 coral species with biogeographical distributions in Southwest Madagascar. Traits and attributes are separated by a dash. Trait attributes are coded as a binary matrix and are formatted for import into R.

1.1.3. All Traits –Southwest Madagascar

The 26 coral traits and 136 trait attributes used in this dissertation for the 231 species present in Southwest Madagascar. Traits and attributes are separated by a dash. Trait attributes are coded as a binary matrix and are formatted for import into R.

1.1.4. Sediment rejection traits

Sediment-rejection trait data for 42 species of coral present on the Great Barrier Reef (Stafford-Smith and Ormond, 1992). Trait attributes are coded as a binary matrix and are formatted for import into R.

1.1.5. Reproductive data

Updated reproductive trait data for over 1500 coral species. Published and updated by Baird et. al. (2009). This data will need formatting prior to import into R.

1.1.6. Carpenter data

Environmental sensitivity data for 845 coral species. Published by Carpenter et al. (2008). This data will need formatting prior to import into R.

1.2. Coral Point Count related files

1.2.1. CPCe code

The CPCe code file used for identification of coral species in Southwest Madagascar.

1.2.2. Converting CPCe data to csv files

The Unix shell script used to compile the CPCe files into a .csv file for use in R. Instructions for how to run the code are included in the folder.

1.3. R scripts

The R scripts required for calculating *Tdis*, *Rdis* and associated graphical tools are contained within this annotated R file.