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Analysis of recovery patterns of Indian Ocean coral reefs through examination of scleractinian communities and populations

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Declaration

I hereby declare that the work described in this thesis was carried out by me, under the supervision of Prof. C. R. C. Sheppard, with the exception of those instances in which the contribution of others has been specifically acknowledged.

Additional unpublished third-party data analysed in this thesis were collected by collaborating colleagues as follows. Where third party data have been used for comparative and analytical purposes, this use is explicitly acknowledged. Further details are given in the methods section of this thesis.

- Coral community data from the Outer Seychelles, Northwest Madagascar, and Al Wajh, Saudi Arabia, were collected by Dr. D. Obura in 2008, as part of the *IUCN-World Conservation Union Climate Change and Coral Reefs (CCCR)* Indian Ocean research initiative.
- Benthic composition data from Farasan Banks, Saudi Arabia, were collected by Dr. T. Roupael in 2009, as part of a Living Oceans Foundation research expedition to the Red Sea.
- Benthic composition data from the Granitic Seychelles were collected by Dr. S. Wilson in 2008 as part of a reef research expedition undertaken in collaboration with the Seychelles Fishing Authority.

Throughout this thesis, all other sources of information have been specifically acknowledged and cited, with full references to published literature detailed in the bibliography.

Some of the findings and data presented in this thesis have been published separately in the publications listed and reproduced in Appendix VI.

I hereby confirm that neither this thesis, nor any information contained within it, have been submitted for a degree at any other university.

Signed

Date

Alasdair R. Harris

20th May 2010

Abstract

This thesis examines the colony size structure and taxonomic composition of coral communities from eight regions of the Indian Ocean approximately 10 years after thermal stress-induced mass mortality events. Coral community composition and population structure differed widely within and between regions, reflecting the different climatic and anthropogenic impacts experienced by each over the past decade.

Coral communities in most areas started from a similarly depleted condition but after 1998 their recovery trajectories varied significantly, reflecting different surviving adult communities and continuing, different local stressors; some have remained highly depleted, while others have shown marked recovery. Profound differences between coral communities at intra and inter-regional spatial scales are identified and related to diversity and taxonomic composition, colony abundance, surface area, size frequency distributions, and population demographic parameters within taxa. These are analysed through multivariate techniques and univariate graphical representations to illustrate the significantly different size frequency distributions, taxonomic composition, taxonomic richness and dominance patterns at different spatial scales.

A novel technique is assessed for surveying juvenile coral communities, using ultraviolet light, which causes new, growing tissue to fluoresce. This method significantly increases detected juveniles, with important consequences to size frequency patterns and to some previously published views on juvenile densities.

The surveying methodologies used are far more revealing than most commonly-used conventional benthic assessments such as intercept surveys, cover values and diversity, which rarely capture discriminatory information on overall composition of coral communities, let alone the structure of populations within them. These colony size-based studies of individual genera are extremely sensitive for interpreting spatial and temporal variations in reefs and greatly enhance understanding of coral reef condition and complexity.

The spatial differences demonstrate the applicability of the methods for advising reef management, specifically in identifying areas where ecological resilience is impeded by recruitment failure. Long-term consequences of changes in coral communities may include reduced ecological functional redundancy, reduced structural complexity, reduced carbonate accretion and reef growth, and impaired recovery potential.

Glossary of terms used in this study

Reef region

The geographic region or country within which reef sites were selected.

Reef site

A discrete and normally geomorphologically-distinct coral reef at which replicate surveys were carried out during this study. In certain cases (such as on Toliara's linear Grand Récif barrier reef), several sites were selected on the same slope of the same reef, however in such cases a minimum distance of several hundred metres was maintained between multiple sites.

Coral community

All colonies of scleractinian hard corals and hydrozoan *Millepora* spp., belonging to all taxa, at a defined reef site or region.

Coral population

The total assemblage of scleractinian hard corals, or hydrozoan *Millepora* spp., within a single taxonomic genus, at a defined reef site or region.

Coral colony

A scleractinian hard coral or hydrozoan *Millepora* spp., colony consisting of autonomous skeleton with living tissue. If partial mortality has separated living tissue within the same colony, this colony is still considered to be one coral. Colony size was measured independently of the size of continuous unbroken coral tissue to ensure consistency with past studies (Bak and Meesters 1998).

Juvenile and Adult

Because definition of a coral 'juvenile' varies considerably between studies, interpretation of the term is commonly arbitrarily fixed at a maximum colony diameter. Here 10cm is used to ensure consistency between data from this study and CCCR methodologies. The term 'adult' coral is used for colonies greater than 10cm.

Colony density

The number of separate hard coral colonies per unit area, typically per m².

Coral surface area

The two-dimensional surface area of a coral, calculated as a circle from r as half the longest axis across the surface area of the colony. This axis is measured over the surface of the colony to take account of raised features of the colony, and is not based on an aerial-view two-dimensional or flat planar cross-sectional area. Surface area in this context does not account for the individual branches, plates, fronds or verrucae making up certain structurally complex colonies; it represents a simplified 'rubber-sheeting' view of colony size, based on a rapid assessment method that favours sampling large numbers of colonies.

INTRODUCTION

1 Overview of research

1.1 Regional differences in coral communities following ocean warming events

Dramatic mortality events have been observed throughout the world's coral reefs in recent years causing a marked decline in global reef condition. The primary drivers of reef mortality before around 15 years ago were considered to be a wide range of localised forms of pollution and over-extraction of, for example, herbivores. However, while these continue and in most regions increase, since approximately 1998 additional degeneration of reef health has come from sea water warming spikes. This climate-related degradation has been exacerbated by direct human impacts, which have weakened the ecological resilience of all but the most isolated reefs.

These growing global climate change and direct anthropogenic stresses are driving shifts in coral assemblages worldwide. Changes in the composition of coral communities have profound ecological impacts on coral reefs and on the human communities dependent on them. Recent studies suggest that 32.8% of coral species are at an elevated risk of extinction, with the family Acroporidae – the primary architect of Indian Ocean reefs - showing a higher proportion of threatened and near threatened species than other families with dominant reef-building species (Carpenter et al. 2008). These long-term changes in coral communities can also adversely affect reef architecture, habitat complexity and reef growth. Resulting reef degradation can then have catastrophic consequences on coral reef-derived ecosystem services. These impacts are in turn likely to affect the resilience and recovery potential of coral reefs, and thus their ability to cope with future climatic and anthropogenic impacts.

Predicting and modelling population dynamics and the future assemblages of coral communities in the face of growing levels of disturbance is of profound relevance to coral reef managers seeking to safeguard ecological resilience of coral reefs and related marine ecosystems.

Few quantitative studies have been undertaken to describe coral communities or the composition of assemblages of hard coral populations making up coral reef communities after the climate-induced mass coral mortality event of 1998. There is considerable uncertainty therefore regarding the nature and likely long-term consequences of shifts within scleractinian communities, so that changes in coral community composition and population structure following disturbance events remain poorly understood. The western Indian Ocean is amongst the least studied coral reef areas globally in this respect as well as being amongst the most stressed from direct human impacts such as overfishing (Obura 2008).

This research analyses data on coral community composition and population structure across eight regions in the Indian Ocean region that have experienced widely differing stress and disturbance histories in recent years. The data also address the paucity of information on coral community composition and population structure globally, and in particular in this previously poorly studied region. Data used in this study were collected between 2006 and 2009.

1.2 Research questions

1.2.1 Nature of coral community changes

Is the composition of Indian Ocean hermatypic coral communities changing in response to increased climatic and anthropogenic stresses, compared to available historical data documenting the condition of Indian Ocean reefs? What patterns or trends may be identified in intra-specific (population) and/or inter-specific (community) responses of corals?

Framework shift

Are reefs experiencing a framework shift, with overstory species being replaced by understory taxa?

Strategy shift

Are hardy, disturbance-adapted species replacing less hardy species? For example, is an *Acropora*-agaricid or *Acropora*-faviid shift taking place?

Size shift

Are coral communities or populations becoming increasingly skewed towards larger or smaller colony sizes in response to ongoing environmental stress and disturbance?

1.2.2 Causes, extent and duration of these changes

If changes in coral communities are taking place, are similar patterns being observed between regions? If so, can these changes be related to current and past climatic and anthropogenic stress histories at survey regions?

1.2.3 Ecological implications

What long-term ecological consequences might result from coral community composition changes? Will coral community changes reduce biodiversity, functional redundancy and/or niche availability for coral-dependent species, such as reef fish? Will these changes affect coral reef resistance and/or resilience to climatic change?

1.2.4 Accretional implications

What long-term physical and geomorphological consequences might result from changes in coral communities? Will changes affect rates of reef growth and/or sand production, or resistance to bioerosion, predation, sea level rise and storminess?

1.2.5 Interpreting coral communities

To what extent do data describing coral populations and communities improve our ability to detect changes within and between reef communities? Does monitoring coral population structure and community composition provide new insight into reef health and/or complexity?

1.2.6 Methodological advances

How do the results of this study improve understanding of the relative benefits of different sampling and methodological approaches for surveying coral communities? To what extent does the use of ultraviolet census techniques enhance detection of juvenile colonies?

2 Responses of coral communities and populations to environmental stress

2.1 Global Climate Change and coral reefs

Globally, coral reefs are deteriorating and diminishing on a scale that predicts the loss of 60% of coral reefs by 2030 (Wilkinson 2008). Twenty percent of the world's 285,000 km² of known reefs are now degraded beyond the point of recovery (Riegl 2009; Pennisi 2007). In recent years the concept of anthropogenic climate change has evolved from being a scientific hypothesis to irrefutable and empirically demonstrable fact; an unambiguous, unequivocal reality that places unparalleled importance and urgency on the management of vulnerable ecosystems worldwide. The forecast extent, rate and impacts of anthropogenic global climate change on coral reefs worsen with each successive projection, with many of the worst-case 2007 IPCC projections, "or even worse", being already realised (Kintisch 2009).

Detrimental human influences on coral reefs are increasing and diversifying at unprecedented rates. Given forecast trends of global population growth, greenhouse gas emissions and marine resource use, these impacts show no signs of abating. Management has failed to stem this collapse beyond a few isolated local examples, and many regional-scale reef systems are considered to be ecologically moribund.

The latest forecasts (Veron et al. 2009) predict an inevitable and irreversible decline in reef condition over the coming decades, with coral reefs largely becoming erosional structures within the next century, in both physical and ecological decline, if anthropogenic CO₂ emissions continue to rise. The loss of coral reefs will inevitably bring about cascading effects on other marine ecosystems, as well as feeding back to climate and ocean chemistry. These domino effects are now considered likely to bring about earth's sixth mass extinction event. Consistent with contemporary observations, principal drivers of past mass extinctions of corals are all linked in some way to changes in the carbon cycle (Veron 2008).

Coral reefs are amongst the most biodiverse habitats on earth. Although they make up only 0.2% of the world's oceans, reefs harbour approximately one third of described marine species (Veron et al. 2009). Yet the diverse perils facing coral reefs threaten not only crucial biodiversity hotspots, but also an economically critical resource that generate up to \$375 billion per year in ecosystem services and revenue, mainly through fisheries and tourism (Pennisi 2007; Martinez 2007). Approximately 0.5 billion people, around 15% of the world's population, live within 100 km of coral reefs, which account for 25% of fish catches in developing countries (Bryant 1998; Pomerance 1999). Coral reef fisheries landings are estimated to be 64% higher than can be sustained (UNEP 2006). Given projections of coastal population growth an estimated additional 156,000 km² of coral reef is required to support human reef fishery requirements by 2050 (UNEP 2006). Fishing yields and coastal food security will be drastically impaired as reef viability continues to diminish.

There are four principal detrimental impacts of global climate change on coral reefs: increased temperature, increased acidity, sea level rise and increased storminess.

2.1.1 Temperature

Rising atmospheric greenhouse gas concentrations have driven increases in average global ocean surface temperatures of 0.7 °C since the start of 20th century (IPCC 2007). Global average surface temperatures are predicted to rise a further 1.8 – 6.4 °C by 2100 under the different emissions scenarios of the Intergovernmental Panel on Climate Change (IPCC), driving marine temperatures to thresholds that have not occurred since the Pliocene epoch (5.3-1.8 Ma) (IPCC 2007). Current and forecast temperature changes far exceed those that occurred during the last glacial-interglacial climatic transition (5-7 °C over 5000-7000 years), which resulted in profound changes to coral assemblages including the rapid extinction of two dominant Caribbean species (Pandolfi et al. 2005; Hoegh-Guldberg 1999).

Corals are extremely vulnerable to thermal stress, and have low adaptive capacity. In the face of an unseasonably high water temperature increase of 1 to 2 °C for 3 to 4 weeks, the obligatory symbiosis between corals and their endosymbiotic dinoflagellates, *Symbiodinium* spp., breaks down, resulting in coral bleaching. Without

Symbiodinium corals lose their primary source of nutrition, and quickly die if temperatures do not return to a point at which they are able to recapture *Symbiodinium*, either from free-living dinoflagellates in the water column or from residual symbionts within the coral tissue. Sporadic incidents of mass coral bleaching resulting in mortality on broad geographic scales were first recorded when CO₂ levels reached ~340 ppm. Current levels of CO₂ (~391.06 ppm) (NOAA ESRL, May 2010) are forecast bring about more frequent episodes of widespread coral bleaching and mortality, unless there is thermal adaptation or acclimatisation by corals (IPCC 2007).

Coral cover fell markedly across the Indian Ocean after the 1998 mortality event, when some of the warmest sea surface temperatures (SSTs) in recent history coincided with the strongest El Niño on record. Many reefs throughout the world's tropical and subtropical oceans suffered near complete eradication of living coral. Some of the coral fatalities occurred in corals of up to 700 years of age on the Great Barrier Reef, indicating that 1998 is likely to have been the worst mortality episode for several hundred years (Hoegh-Guldberg 1999). Coral mortality was so marked in some locations that a rotting odour of decaying coral tissue was evident for weeks during the summer of 1998 at many reefs after the bleaching event (Loya et al. 2001). Thermal tolerance of hard corals is predicted to be exceeded annually within the next few decades, with severe bleaching episodes on a par with the 1998 event becoming unexceptional within 20 years (Hoegh-Guldberg et al. 2007).

Such mortality may have secondary impacts to coral bleaching including increases in coralivory by concentration of coral predators on remnant surviving colonies, increased susceptibility to disease in stressed colonies, and increased bioerosion as a result of the abundance of dead reef framework (Baker et al. 2008).

Absolute mortality is corals' most extreme response to bleaching stress. After moderate bleaching, corals may survive and recover either residual or free-living dinoflagellate symbionts. However surviving corals normally show lowered fecundity, reduced growth and calcification rates and increased vulnerability to pathogenic diseases (Hoegh-Guldberg 1999; Harvell et al. 1999). Thermal stress has been shown to decrease reproductive capacity of diverse genera from several families, including

Acroporidae, Faviidae and Mussidae (Hoegh-Guldberg 1999). Depressed fecundity results in further setbacks to recovery processes, which are likely to remain inhibited in the face of regular bleaching. Reduced growth rates of corals are likely to increase the frequency and duration of competitive interactions between corals and other benthic groups such as macroalgae (Mumby et al. 2007).

2.1.2 Ocean acidity

Approximately 25% of anthropogenic carbon dioxide emissions enter the world's oceans, decreasing the concentration of dissolved carbonate, ocean pH and carbonate saturation levels (Hoegh-Guldberg et al. 2007).

Climate models predict that oceanic pH may decrease by up to 0.4 pH units by 2100, and that dissolved carbonate and carbonate saturation levels may fall below the minimum thresholds for calcification and carbonate accretion within the next century. Estimates of precisely when this threshold will be reached vary depending on the climate models and scenarios employed, however according to the IPCC lower range emissions scenarios, this will occur approximately when $[\text{CO}_2]_{\text{atm}}$ reaches 450-500 ppm (Hoegh-Guldberg et al. 2007; Raven 2005). Experimental studies have shown a 40% reduction in aragonite formation by raising pre-industrial $[\text{CO}_2]_{\text{atm}}$ to 560 ppm, and carbonate accretion on coral reefs is known to shut down at aragonite saturation values of 3.3 in today's oceans ($[\text{CO}_2]_{\text{atm}}$ 480 ppm; $[\text{CO}_3^{2-}]_{\text{aq}} \sim 200 \mu\text{mol kg}^{-1}$ seawater) (Hoegh-Guldberg et al. 2007). Calcification rates in corals are predicted to decrease by $30\% \pm 18\%$ by the time twice pre-industrial levels of atmospheric CO_2 are reached (30 - 50 years) (ISRS 2008). Consistent with these projections, the fossil record shows a notable absence of marine calcifiers, including reef-building corals and calcareous algae, during the early Triassic epoch, when $[\text{CO}_2]_{\text{atm}}$ increased to 5 times today's levels during the Permian-Triassic extinction event (Hoegh-Guldberg et al. 2007).

Given recent global climate change trends and predictions, reductions in calcification rates are likely to result in a decrease in coral growth rates, defined as the product of a coral's linear extension rate and skeletal density. Calcification rates of reef communities dominated by living coral and coralline algae vary little with changes in the composition or relative abundance of species, and are estimated to be up to 10 kg

$\text{CaCO}_3 \text{ m}^{-2}\text{y}^{-1}$ (Kinsey 1991). If current levels of anthropogenic CO_2 emissions continue to rise unabated, calcification will decrease, potentially to zero, leading to a net loss of CaCO_3 per unit reef area. Decreasing growth rates of 14% since 1990 (unprecedented in a 400 year timescale) have recently been recorded on corals of the Great Barrier Reef, with similar observations from the Indian and Atlantic oceans; a possible consequence of increasing ocean acidification (De'ath et al. 2009; Tanzil et al. 2009; Bak et al. 2009).

Under conditions of reduced calcification, a coral may only be able to maintain either skeletal density or linear extension rates by neglecting the other factor. Corals responding by reducing skeletal densities will lose durability, becoming increasingly fragile and vulnerable to erosion and grazing, while corals reducing extension rates will be less able to compete for habitat space within the benthos, and less able to resist natural erosive forces and grazing.

Either manifestation of reduced coral growth rates would inevitably result in diminished reef stability and structural complexity, in turn reducing habitat condition and diversity, reef rugosity, fish density, fisheries productivity and wave attenuation potential (Hoegh-Guldberg et al. 2007; Wilson et al. 2006). The impacts of reduced scleractinian skeletal density on reef structure may be particularly damaging given projected increases in storm intensity and frequency (IPCC 2007). The effects of reduced skeletal growth on juvenile life stages, settlement and recruitment of calcifying organisms are largely unknown, however it is likely that such impacts will compromise survivorship of recruits (ISRS 2008).

Dissolution rates of carbonate rock and reef sediments will increase with decreasing ocean pH. Combined with the effects of reduced biological carbonate accretion, reef building will be further compromised by increased rates of removal of the underlying carbonate reef structure (ISRS 2008).

In the face of reduced aragonite saturation levels, greater allocation of resources towards increasingly energetically expensive carbonate production by corals would divert corals' energy expenditure away from other life processes such as reproduction

and combating infection. Inadequate maintenance of such critical processes is likely to weaken reef resilience and increase vulnerability to other threats (Hoegh-Guldberg et al. 2007).

The effects of changes to ocean chemistry on other carbonate-producing organisms may have further indirect detrimental impacts to reef corals. Coralline algae, a major constructional feature of reefs and favoured settlement substrate for many coral planulae, is particularly sensitive to ocean pH (Kuffner et al. 2007), and, like corals, is likely to be threatened by predicted increases in ocean acidity. Threats to the growth of calcifiers on coral reefs will favour the growth of competing benthic organisms, particularly macro-algae; fast-growing marine plants which compete with corals and coralline algae for available space on the benthos, in doing so further inhibiting coral settlement, growth and reproduction. The combined factors of diminished growth of coral and coralline algae and increased competition between benthic calcifiers and macro-algae are likely to increase reef vulnerability to thermal stress and anthropogenic disturbance.

2.1.3 Sea level rise and increased storminess

Rapid increases in sea level of 23 to 51 cm are forecast by 2100 within IPCC scenario A2, along with increases in the frequency and severity of tropical storms and cyclones in the Indian Ocean (IPCC 2007). Reef growth is the sum of both constructive and destructive processes over time. Although natural coral growth rates of rapidly-growing corals such as *Acropora* ($\leq \sim 20 \text{ cm y}^{-1}$) greatly exceed current and predicted rates of sea level rise ($\sim 1 \text{ cm y}^{-1}$), slower-growing corals such as *Porites* ($\leq \sim 1 \text{ cm y}^{-1}$) may be particularly vulnerable (Barnes 1973).

However, colony growth rates should not be confused with vertical reef accretion rates, which commonly approximate 4 mm yr^{-1} (Buddemeier and Smith 1988). Physical and bio-erosion of lithified platforms in Aldabra Atoll, western Indian Ocean, was estimated to be up to 4 mm yr^{-1} , with bioerosion the primary eroding force (Trudgill 1976). Anticipated rates of sea level change this century are forecast to be greater than normal rates of reef growth ($\sim 6 \text{ mm yr}^{-1}$) (Montaggioni 2005).

Weakened and eroding reefs will be particularly vulnerable to sea level rise, increased storminess and erosive forces, which are likely to struggle to maintain growth rates necessary for corals to retain their current depth positions within the photic zone of the water column. Loss of reef material through coral mortality and erosive forces from the top of a reef will have the same effect as an increase in sea level of the equivalent amount (Sheppard 2006). Increased storminess is thought to be already affecting some reef regions, such as the Great Barrier Reef, both through high energy storms (due to increased ocean surface temperature) and destructive rainfall (Nott and Hayne 2001; GBRMPA 2009; Webster et al. 2005).

2.1.4 Acclimatisation and adaptation

Corals and their symbionts are able to respond physiologically to changes in environmental factors, for example by altering metabolic and other cellular processes to operate under new conditions. Responses take place quickly, normally within hours or days, since corals experience wide variation in environmental conditions during a normal diurnal cycle (Gates and Edmunds 1999).

For example, the concentration of photosynthetic pigments within zooxanthellae changes in inverse proportion to levels of light intensity. In the event of excessively high light intensities, which can result in photoinhibition of zooxanthellae, corals' symbionts are able to engage a series of protective 'quenching' mechanisms, involving changes in xanthophyll pigments, to reduce the potentially detrimental impact of high light intensity (Hoegh-Guldberg 1999). *Pocillopora* and *Porites* colonies in shallow lagoon sites in Kenya have been observed to exhibit much lower bleaching and paling than the same species in deeper sites. This is thought to be on account of acclimation of the shallow corals to the more variable and extreme thermal and light conditions typical of the shallower reef environments (Grimsditch et al. 2008).

Such mechanisms of acclimatisation serve to demonstrate corals' considerable intrinsic biological flexibility, a requirement for survival in a heterogenous diurnally changing marine environment. This innate versatility provides corals with a margin for acclimatisation to certain stress factors, such as moderate increases in temperature. However, compensatory metabolic changes are constrained genetically, and species

are unable to adjust physiologically to extreme changes in environmental conditions. Environmental change since the industrial revolution may have brought corals close to their limit of physiological acclimatisation, and that recent mortality episodes are a result of environmental stresses going beyond this threshold (Hoegh-Guldberg 1999). Moreover, adaptation of corals and zooxanthellae results from a genetic, rather than physiological, response to selective pressure (Douglas 2003). A coral or symbiont's ability to adapt its genotype to better suit changing environmental conditions relies on opportunities to introduce variation into the population gene pool. Such opportunities are limited by the generation time of the species in question.

Adaptation scenarios and predictions need to include consideration of the adaptive capacity of both the coral host and the *Symbiodinium* symbiont, although studies indicate that coral phylogeny is likely to be a more reliable correlate than symbiont genotype for identifying coral vulnerability to thermal stress (McClanahan 2004). Unlike short-lived, fast-reproducing species such as bacteria, which are able to adapt and evolve over periods of days, evolutionary changes in longer-lived, slower-reproducing species such as corals take place over decades and centuries. As such, corals are considered to have low adaptive capacity. This hypothesis is confirmed by the fossil record, which shows that species with short generation times were able to resist extinction when slower-reproducing species such as corals were heavily impacted by mass extinction episodes (Copper 1994).

Nevertheless, corals are capable of exploiting extreme environments, and in many areas have successfully adapted to high temperature regimes that would kill individuals of the same species habituated to living in milder environments (Coles et al. 1976). Evidence of corals' ability to adapt to different temperature regimes is exhibited by individuals of the same species occurring at different latitudes, or within reef environments exposed to widely different temperature regimes. In some cases colonies are able to tolerate complete atmospheric exposure at low tides; severe environmental stress that would kill colonies of the same species adapted to more benign environments. In the aftermath of the 1998 mortality episode, juvenile *Acropora* colonies in Japan were observed to survive in the intertidal zone despite

being exposed to high irradiance, direct exposure and desiccation during spring low tides (Loya et al. 2001).

Adaptations are likely to have occurred as a result of selective evolutionary processes acting over long time scales. When exposed to non-lethal environmental change, species previously adapted to a benign environment are likely to experience selective pressure leading to adaptations over hundreds of generations; centuries if not millennia. Corals today have experienced rapid environmental change over much shorter time scales, and mortality-inducing warming episodes have regularly crossed these thresholds. As a result, six major bleaching episodes have occurred since 1979, with corals in some regions suffering serious bleaching every time (Hoegh-Guldberg 1999).

Heavy bleaching recorded in the Seychelles and Chagos islands in 2004 resulted in severe mortality of new recruits. Surveys in Chagos recorded severe bleaching of 65% of newly recruited *Acropora* (Sheppard et al. 2008). Such observations indicate that the new recruits, presumably spawned from survivors of the 1998 mortality, had not adapted genetically to cope with such conditions. This suggests that the genetic structure of such coral communities had not adapted to tolerate thermal stress rapidly enough to resist effectively the degree and frequency of extreme climatic events experienced at these sites.

Thus although phenotypic changes in dinoflagellate symbiont communities may confer some resistance to bleaching, there is little evidence that corals or their symbionts have been able to adapt rapidly to coral bleaching, or to the levels of thermal stress that are forecast by climate change models and scenarios (Hoegh-Guldberg et al. 2007). It is improbable therefore that future adaptation will protect corals from forecast climate change, since predicted temperature changes are likely to be too great and too rapid for even the hardiest corals and zooxanthellae (Hoegh-Guldberg 1999).

2.1.5 Increasing rates of change and diminishing recovery periods

The recovery time of coral reefs following major mortality-inducing perturbations, including cyclones and mass bleaching, has been estimated to range between 1 and

100 years (Connell et al. 1997; Harmelin-Vivien 1994). These differences reflect not only the considerable variations between different reef environments, impacts and recovery trajectories, but also the range of variables used to monitor and determine recovery of species and ecosystems.

Given that corals show reduced growth and fecundity after stress, a reduction of the recurrence interval between broad-scale extreme climatic, storm, disease, predator or anthropogenic disturbances will result in corals being stressed in an already compromised state, in turn causing more frequent, chronic setbacks to coral reef recovery processes. For example, the predicted increased frequency of bleaching events may reduce corals' ability to re-establish viable breeding populations in between mortality episodes. Consequently, increases in the frequency of environmental perturbations such as bleaching and storm disturbance, as predicted by global climate change scenarios (IPCC 2007), are likely to play as important a role in influencing reef recovery trajectories as will increases in absolute environmental parameters such as sea temperatures.

2.1.6 Synergies and compounding anthropogenic impacts

Predicting responses of marine ecosystems and corals to global climate change is complex, confounded by numerous feedback processes (Hoegh-Guldberg et al. 2007). Local threats and stresses to coral reefs, such as unsustainable biomass removal, reduction of water quality, by increasing levels of sedimentation, pollution, toxins and disease, may compound the impacts of climate change. The threats of climate change are greatest where reef resilience is already weakened by such synergistic anthropogenic stress factors (Hoegh-Guldberg et al. 2007).

2.2 Interspecific responses to environmental stress: differential mortality of species and scleractinian community shifts

Coral reef communities are highly dynamic, in particular in the aftermath of environmental disturbances. Different coral species show variable responses to thermal stress based on evolutionary and environmental history, physiological acclimatisation ability, growth form and depth (Gates and Edmunds 1999; McClanahan 2004).

Approximately one third of hermatypic corals face increased risk of extinction as a result of climate change and direct anthropogenic impacts (Carpenter et al. 2008); a higher proportion of threatened species than any terrestrial animal group apart from Amphibians. From a total of 845 zooxanthellate reef-building species assessed in a recent study, only 80 species were considered to be resistant to bleaching. These were primarily from the genera *Favia* and *Porites*. The families Caryophyllidae, Astrocoeniidae, Merulinidae and Fungiidae had the lowest proportions of species considered threatened. Conversely, nearly 50% of species of Acroporidae, Euphylliidae and Dendrophylliidae are considered threatened (Carpenter et al. 2008). At a local level, while some coral species may be extirpated by bleaching stress (Sheppard et al. 2009), others may survive apparently unharmed (Marshall and Baird 2000).

Like susceptibility to *Acanthaster planci* predation, observations suggest that the taxa most vulnerable to bleaching are fast-growing, often short-lived, space colonisers (McClanahan et al. 2004). Most reports in the aftermath of the 1998 mortality episode showed that branching coral species were typically the first to bleach and die (Wilkinson 2000). Some reef sites experienced almost total loss of hard and soft coral cover, with branching corals such as *Acropora* - the largest and amongst the most widespread extant genus of reef building coral - commonly showing generally far higher levels of mortality than massive, submassive or encrusting species (McClanahan et al. 2004; McClanahan 2000). Once the most diverse and abundant coral genus throughout the world's oceans, *Acropora* is an increasingly scarce component of tropical reef communities, with declining species diversity within the genus.

A number of studies have shown coral morphology to have a major influence on temperature tolerance, with considerable differences in colony survival relating to corals' growth forms and taxa. This pattern of increased susceptibility to mortality of branching taxa has been recorded at numerous geographic reef localities throughout the Indopacific and Atlantic tropical and subtropical oceans in recent years. Scleractinian community shifts in many reef areas have been a result of differential mortality between taxa, particularly in the aftermath of the 1998 mortality episode (Hoegh-Guldberg 1999; Grimsditch and Salm 2005). There is growing evidence that differential susceptibility of coral taxa to bleaching, and perhaps differential

recruitment following mortality, is now leading to profound changes in community composition in the recovering assemblages.

2.2.1 Pacific Ocean

During the 1998 mortality event, genus-specific mortality was observed in the central Great Barrier Reef (Hoegh-Guldberg 1999), with stagshorn *Acropora*, generally considered to be one of the most sensitive genera to slight increases in water temperature. Studies of bleaching response of corals on the Great Barrier Reef in 1998 showed that the faviid corals *Platygyra daedalea* and *P. lobata* took longer to bleach and die than the acroporid corals *Acropora hyacinthus* and *A. millepora* (Baird and Marshall 2002). Finely branched corals were most susceptible to bleaching and subsequent mortality in the southern Japanese islands, while massive and encrusting colonies generally survived (Loya et al. 2001). Studies in the aftermath of the mortality event showed acroporids to be on the whole far more vulnerable to bleaching mortality than faviids and poritiids (Fujioka 1999).

Comparison of shallow water hard and soft coral community structure at Sesoka Island, Japan, between 1997 and 1999 recorded a dramatic halving of coral species recorded in quadrats between these dates, constituting a near-elimination of living coral cover from 34.4% in 1997 to 0.2% in 1999, equivalent to 99% decrease (Loya et al. 2001). The island also showed clear differential survival of species, with distinct 'winning' and 'losing' taxa linked to colony morphology and possibly tissue-thickness (Loya et al. 2001). Branched *Acropora* corals, once the most abundant and prolific species at most locations, were heavily impacted, and several additional species suffered local extinction between 1997 and 1999. The differential mortality of species and overall dramatic decrease in total living coral cover resulted in marked increases in the relative contribution of certain less vulnerable species within the depauperate community: *Porites lutea*, *P. lobata* and *Goniastrea aspera*, for example, increased their relative contribution to the total abundance by 3.4-, 2.1- and 2.8-fold respectively. *Porites lutea* increased its relative contribution to living hard coral cover from 16.3% in 1997 to 43.8% in 1999, and its relative contribution to the total abundance from 3.3% to 11.2% (Loya et al. 2001).

2.2.2 Indian Ocean

Throughout the Indian Ocean, niches formerly occupied by *Acropora* are being progressively replaced by corals with different life history strategies, including previously subordinate taxa, as well as by non-carbonate accreting producers such as seaweeds and zooanthids (Sheppard and Obura 2005; Harris et al. 2010). Many of the observations of dramatic reductions in *Acropora* also apply to *Montipora*. Coral assemblages have been observed to shift towards conditions of dominance by faviids and *Porites* at numerous sites in the region (Edwards et al. 2000; Loch et al. 2002; Spencer et al. 2000).

Surveys carried out in the aftermath of the 1998 coral bleaching event in the Maldives, where the extent of coral mortality was amongst the highest in the world showed the encrusting agaridid *Pavona varians* to be the main constituent of the recruit community, and recorded a shift in dominant species in the overall coral community from acroporids and pocilloporids to agaricids (Schuhmacher et al. 2005). The same study at Fadiffolu atoll from 2000 to 2002 showed the relative composition of Agariciidae to increase from 49% to 74%, while *Acropora* and Pocilloporidae decreased from 22% to 3% and 17% to 1% respectively (Schuhmacher et al. 2005).

Edwards et al. (2000) recorded a post-bleaching shift in species composition in the Maldives “from a 95% pocilloporid / acroporid dominated coral community to a 92% agariciid / poritiid / faviid one” (Edwards et al. 2000). Similar post-bleaching *Pavona* dominance was recorded elsewhere in the Maldives in the aftermath of the mortality episode (Loch et al. 2002; McClanahan 2000). Other transects carried out in the Maldives 21 months after the 1998 mortality episode identified *Goniastrea* spp., *Porites*, *Favites flexuosa* and *Podabacia crustacea* as the dominant recolonising coral species (Loch et al. 2002).

Studies in the Maldives in 1999 and 2000 showed that *Acropora palifera*, *Stylophora*, *Seriatopora*, branching *Porites* and *Millepora* (*P. nodifera*, *P. compressa*, *M. tenera* and *M. intricata*) may have been locally extirpated, while the surviving dominant corals were massive and columnar Poritidae, Faviidae, and Acroporidae (*Astreopora myriophthalma* and *Porites lutea*, *Porites cylindrica* and *P. rus*) (Loch et al. 2002;

McClanahan 2000). Surveys carried out 21 months after the 1998 mortality episode identified *Pavona*, *Leptoseris*, *Goniastrea* spp., *Porites*, *Favites flexuosa* and the brooding coral *Podabacia crustacea* as the dominant survivors and recolonising coral species. These studies also showed that agariciids, faviids and poritiids (notably *Pavona*, *Leptoseris Coscinarea*, *Porites* and *Synarea*), dominated the recruit community during the early stages of recolonisation (1999), with *Acropora*, *Montipora* and *Pocillopora* recruits being comparatively scarce (Loch et al. 2002; McClanahan 2000; Schuhmacher et al. 2005). Roughly one third of new settlers recorded in one study were agariicids (Loch et al. 2002). Observations that the dominant corals in 1999 differed from the pre-mortality coral community led to the hypothesis that Maldives reefs might be following a recovery trajectory favouring coral genera that did not dominate the pre-1998 reef community (McClanahan 2000).

In Chagos the near total elimination of *A. palifera*, formerly the dominant wave-resistant architectural reef crest species throughout the archipelago, resulted in a drop of shallow reef height of approximately 1.5 m (Sheppard 2006). Like Chagos, many Seychelles reef flats were covered, pre-1998, with 0.5 m stagshorn *Acropora* that reached low tide level. These thickets are now dead in most areas (Sheppard 2006; Sheppard et al. 2005).

In the Granitic Seychelles coral bleaching in early 1998 led to mortality of 85-95% of coral cover, with the genera *Acropora* and *Pocillopora*, principal architectural components of the reef structures, suffering the highest levels of mortality. Following subsequent bleaching events in 2002 and 2003, slow growing corals such as massive *Porites* and *Goniopora* were observed to become increasingly dominant genera, suffering only temporarily arrested growth from bleaching events that brought about significant losses in branching and encrusting taxa (Engelhardt 2004; Engelhardt et al. 2002).

Surveys in the southern Seychelles during the 1997-1998 Indian Ocean warming event recorded high levels of bleaching and mortality in branching coral species, in contrast to low levels in encrusting species. Large stands of *Acropora* and *Pocillopora* spp. displayed levels of up to 100% bleaching, compared with only partial bleaching in *Porites*, *Favia* and *Pavona* spp.. Surveys of the carbonate reefs of the Amirantes and

Alphonse islands of the southern Seychelles in 2005 showed live coral cover to be dominated by *Porites* and *Pocillopora* (Hagan et al. 2008). Other studies of coral bleaching in the southern Seychelles in 1998 showed far higher bleaching incidence in *Acropora*, *Pocillopora*, *Galaxea* and *Seriatopora* than in massive corals such as *Porites* and *Pavona* (Spencer et al. 2000).

Corals in Cosmoledo, in the Aldabra group of the outer Seychelles islands, suffered almost total mortality to approximately 10m depth, with around 50% mortality in deeper zones, varying depending on coral taxa. Unlike Acroporid and fungiids, which showed near-ubiquitous mortality, Poritiids and mussids showed appreciable survival of adult corals (Sheppard and Obura 2005). Coral recruitment in Cosmoledo was observed to have recovered rapidly four years after the mortality episode. However, the recruit community was dominated by faviids and *Porites*, which were the most successful surviving taxa. Conversely, the recruit community showed a scarcity of certain previously dominant genera, notably *Acropora*, which had experienced the most serious mortality at all depths surveyed during the study. The results of these surveys resulted in predictions of long-term shifts in identity of dominant coral species of corals in these atolls (Sheppard and Obura 2005).

Surveys of coral reefs within the marine reserves of northern Madagascar, from 2005-2006, show mean *Acropora* cover to be less than 1.7% at all marine parks with the exception of Cap Masoala (4.5%). The main *Acropora* species recorded were submassive and encrusting forms, despite evidence at several sites of large, intact *Acropora* skeletons assumed to be relics of an earlier mortality episode, probably occurring in 1998. The vast majority of non-*Acropora* corals comprised encrusting or massive forms (Harding and Randriamanantsoa 2008).

In the Arabian Gulf immediately following the 1998 event, coral cover in shallow water (<3 m depth) was less than 1% due to near total mortality of vast areas of shallow *Acropora* corals. Her too, faviid corals dominated the juvenile assemblages, as opposed to previously-dominant *Porites* and *Acropora*. These observations led to conclusions that the region's reefs had experienced a shift in their coral communities towards an alternative stable state dominated by faviids. The authors hypothesised that, given the

extreme temperature regimes experienced in the Arabian gulf, the observations recorded may be indicative of likely future changes in other areas of the broader Indian Ocean (Sheppard and Loughland 2002).

Acropora, formerly the most abundant and diverse genus in the Arabian Gulf, has become a rare genus in some areas, with near-total removal of staghorn and tabular forms in most shallow areas, many of which have been replaced by faviids (Sheppard 2006). Surveys of reefs in the Arabian Gulf following the 1998 mortality event recorded fewer than twenty coral species altogether (Sheppard and Loughland 2002). Studies of the temperature tolerances of hard corals from the Arabian Gulf suggest that branching *Acropora*, *Stylophora* and a branching *Porites* (*P. nodifera*) are those most vulnerable to temperature changes (Sheppard et al. 2000).

Similarly, on Kenyan reefs in 2007, *Pocillopora* showed the most bleaching-related mortality of corals at all sites studied. *Porites* colonies also experienced widespread bleaching, but unlike *Pocillopora* this genus showed negligible levels of subsequent mortality (Grimsditch et al. 2008).

McClanahan *et al.* (2004) found significant genus-based responses to bleaching and mortality between reef sites in Kenya and Australia; *Millepora*, *Stylophora* and *Pocillopora* were consistently susceptible, whereas *Cyphastrea*, *Goniopora*, *Galaxea* and *Pavona* were consistently resistant (McClanahan et al. 2004). A western Indian Ocean-wide study of coral community structure, bleaching and susceptibility carried out across 8 countries in 2005, predicted that low-diversity genera with narrow environmental ranges would be most vulnerable to future extinction. Such genera include *Gyrosmlia interrupta*, *Plesiastrea versipora*, *Plerogyra sinuosa*, and *Physogyra lichtensteini* (McClanahan et al. 2007). Observations from the Chagos islands in 2006 suggest that the formerly common monospecific genus *Diploastrea* may have suffered local extinction whilst others, notably *Montipora*, had become extremely rare relative to previously recorded levels. The non-scleractian hydrozoan *Millepora* and blue coral *Heliopora coerulea* also suffered widespread mortality in 1998 (Sheppard 1999).

Massive *Porites* and *Pavona* are considered to be resistant to bleaching relative to most other genera (Mumby et al. 2001; McClanahan et al. 2004). Branching and columnar *Porites* also display high tolerance to bleaching (Grimsditch et al. 2008), and to be successful recruiters after bleaching events (Loch et al. 2002; McClanahan 2000). *Pavona* was the only genus noted to show resistance to bleaching-related mortality in Chagos in 1999 (Sheppard 1999). *Oxypora* and *Pachyseris* have also been observed to show bleaching tolerance (CRC Sheppard pers. comm. in McClanahan et al. 2007).

However, although *Porites* was a dominant survivor at many sites throughout the Indo-Pacific (including the Arabian Gulf) it was heavily impacted too, with branching poritiids exhibiting high degrees of mortality at some sites, and massive colonies showing intermediate bleaching, albeit with higher recovery frequency than branching corals (Kayanne et al. 1999). *Porites* was also the dominant dead species at some sites in the Arabian Gulf (Sheppard 2006).

2.2.3 Atlantic Ocean

In this ocean, coral mortality for many years was attributed to pollution and over-extraction of several kinds. The dominant *Acropora palmata* for example, which previously thrived from the surface to about 4 m depth, largely disappeared in the 1980s due to diseases (Richardson 1998). Losses of three keystone architectural species have been observed at a regional scale on most Caribbean reefs: *Acropora cervicornis* (stagshorn coral), *A. palmata* (elkhorn coral) and *Montastraea annularis*, once primary reef framework builders and special dominants, are now listed under the U.S. Endangered Species Act (Carpenter et al. 2008). As a result of these chronic declines, few extensive *Acropora* assemblages remained to show any mortality from the 1998 warming event.

For example, studies of a lagoonal shoal of the Belizean Barrier Reef showed the coverage of *A. cervicornis* to drop from approximately 70% in 1986 to nearly 0% in 1993 as a result of a mass mortality episode caused by epizootic White Band Disease (Aronson and Precht 1997). Such Caribbean-wide fatal band diseases (fungi and cyanophytes that infect and kill coral tissue) have been attributed to the loss of *A. cervicornis* across the region.

This mortality episode was followed by rapid opportunistic growth of *Agaricia* spp. (lettuce corals) to cover available free space, particularly Belizean endemic *Agaricia tenuifolia*, a thin-bladed anastomosing coral. *Agaricia* had been a minor component of the benthic community in 1986 (covering only 10% reef space), but grew to cover 56% of the benthos within 2 years of the *Acropora* mortality with coverage of other coral species remaining low. A similar trend towards *Agaricia* spp. dominance was observed on other reefs in the region.

Analysis of the *Agaricia* signature left within the available reef sedimentary record showed that no other *Agaricia* layers were deposited during at least the past 3800 years (Aronson and Precht 1997). *Agaricia*'s opportunistic success at these sites may be, in part, a result of its ability to reproduce asexually (through fragmentation) as well as sexually. Conversely, the reproductivity of *Acropora cervicornis*, capable of sexual reproduction only, may have been severely compromised by disease.

2.2.4 Impacts of differential bleaching susceptibility on scleractinian community structure

Given the above observed differential susceptibilities of coral taxa to bleaching, chronic stress, such as repeated mass bleaching is likely to severely transform coral reef species richness and taxonomic composition over time (Berumen and Pratchett 2006).

It can be hypothesised that those genera that survive some bleaching will be the most likely to experience reduced mortality in future bleaching episodes (McClanahan 2004). If, as predicted by climate forecasts, ocean warming becomes a chronic stress to coral reefs worldwide, the most resistant, enduring species will out-compete more susceptible taxa, ultimately reducing formerly diverse coral communities to communities consisting of the hardest constituent species. Therefore under conditions of repeated and increased thermal stress, coral communities are likely to shift to favour dominance of more thermally tolerant species such as *Porites* (Loya et al. 2001), or species whose life history patterns favour rapid recruitment and colonisation, such as *Pavona*.

The inevitable result of such shifts is that species composition will change to favour survivors that did not previously dominate, whilst formerly common species will become less common. Ultimately a “community structural shift” may occur; the result of differential survival of coral species leading to marked changes in species composition and community structure (Loya et al. 2001).

2.2.4.1 Differential susceptibility of reef zones

Almost all coral species and growth forms show preference for certain habitats and zones within a coral reef (Sheppard 2006). Like differences in reef benthic composition, variation in coral ecomorphs and species assemblages occurs with environmental differences including depth, sedimentation, hydrodynamics, wind and wave exposure, bottom topography and turbidity (Riegl and Velimirov 1994; Riegl and Piller 1997; McClanahan et al. 2002).

Thus coral communities vary with depth as a result of diminishing illumination and degree of exposure. In the Caribbean, a number of polymorphic species (such as *Montastrea annularis*, *Agaricia agaricites* and *Porites asteroides*) have been recorded to typically change shape from massive to foliaceous colonies with increasing depth (Hughes and Jackson 1980). Studies from the late 1960s of reefs in Jamaica (whose condition was then comparatively undisturbed) showed plating corals to be common below 20 m, and the most abundant growth form from 30 m to 70 m (Goreau and Wells 1967). Recent studies from the Chagos archipelago also recorded higher prevalence of plating colonies at depth (Harris and Sheppard 2008).

A number of authors have shown that corals in shallow water are more tolerant of temperature extremes and fluctuations than corals in deeper water, which are typically exposed to lower and more constant temperature regimes (Spencer et al. 2000; Sheppard 1999). There is growing evidence that shallow-water lagoonal corals show higher resistance to bleaching mortality events, probably on account of acclimatisation to stress brought about by the naturally high variability of temperature and UV conditions within their typically shallow environments (Grimsditch et al. 2008; Sheppard et al. 2008; Hagan et al. 2008).

For example, corals in sheltered lagoons have been observed to show resistance to bleaching when corals of the same species on adjacent exposed and seaward slopes (exposed to more regular flushing by cooler water) died during mass mortality episodes (Sheppard et al. 2008). Major differences in bleaching responses of corals between shallow and deep lagoonal sites were observed at four sites in Kenya during a mild bleaching event in 2007; deeper sites experienced far higher bleaching than shallower sites. Shallow environments absorb and lose heat faster, and attenuate less light, than deeper sites. These observations suggest that corals exploiting these shallower habitats, which typically experience greater extremes and variations of heat and light, have become more resistant to bleaching stress (Grimsditch et al. 2008).

Empirical observations confirm that corals that regularly experience high stress, such as colonies exposed to the atmosphere at extreme low tides, are better acclimatised physiologically to elevated temperature and UV, although it is not clear whether such acclimatisation is host-based or symbiont-based (Brown et al. 2000; Brown et al. 2002). Thus, combined with differential susceptibility to bleaching, and differential environmental stress based on depth and habitat disturbance, the effects of adaptation and acclimatisation of taxa to high stress environments are likely to further effect surviving coral assemblages and progenitors.

2.3 Intraspecific responses to environmental stress: impacts on coral populations

Although a previously “amazingly neglected” and “hardly touched” field of reef ecology (Bak and Meesters 1999; Bak and Meesters 1998) the study of coral size distributions is increasingly recognised as being useful in coral reef research where high resolution taxonomic study is difficult, for example with corals where species taxonomy is often unresolved (Hughes and Connell, 1987). In contrast to between-species dynamics following environmental perturbations (McClanahan et al. 2004; McClanahan et al. 2007), comparatively little is known about intraspecific changes within populations. Few recent quantitative studies have looked at the life history and population dynamics of hard corals (Hughes and Jackson 1985; Crabbe 2009), and there is little available data on coral demography. However, monitoring spatial and temporal variability of demographic parameters is fundamental to understanding how the populations making up coral communities may be changing in response to disturbance.

2.4 Coral population demography

Size frequency distributions of coral populations provide a sensitive yet little studied means of discriminating changes in coral population dynamics in response to environmental change, and of identifying differences between populations exposed to different degrees of environmental stress. This study sought to utilise coral size frequency data and demographic parameters as a means of interpreting past disturbance through discriminating groups of samples exposed to widely different stress histories across the Indian Ocean.

Mortality and fecundity rates in corals and other clonal organisms are strongly size-dependent (Harrison and Wallace 1990). Susceptibility of corals to most mortality agents decreases with increasing colony size (Hall and Hughes 1996). This is analogous to the 'refuge through size' concept. Juvenile corals experience very high levels of mortality in their earliest post-settlement growth phases (Nozawa et al. 2006). Early life stage corals are more susceptible to disturbance than adults (Tamelander 2002). Adult corals in turn have higher stress tolerance than smaller colonies and are able to endure a number of stresses that would kill newly recruited or juvenile hard corals. Thus coral mortality rates decrease with increasing coral size (Babcock 1985; Babcock and Mundy 1996). This increased colony survivorship may be due to a growing coral's progressively increasing ability to avoid disturbance by factors such as smothering by sediment, predation or fouling.

Many coral species also show a positive relationship between colony size and fecundity (Nozawa et al. 2006; Hall and Hughes 1996). Because smaller colonies are known to be more vulnerable to a number of stressors, including sedimentation and eutrophication, younger corals may allocate proportionately more resources to non-reproductive life-functions such as growth, focusing on reproduction only when the colony has gained a critical threshold size.

In many corals, colony growth is considered to be indeterminate, that is to say colonies will continue to grow indefinitely until succumbing to disease, injury or stress resulting in partial or total colony mortality (Hall and Hughes 1996). Where indeterminate growth of corals is the case, fecundity may rise indefinitely with colony size (Hall and

Hughes 1996). Since coral colony size can influence patterns of mortality and fecundity within reef communities (Baker et al. 2008), population size frequency distributions provide important insight into population processes and ecological disturbances (Hughes and Connell 1987). Coral size-frequency statistics also represent a valuable tool for studying reef degradation, since variables such as skewness of coral populations commonly differ between degraded and healthier reefs (Bak and Meesters 1998).

Coral population structure, as recorded, for example, by size-frequency distribution data, is influenced both by colony growth and the number of colonies within a population; the latter factor being in turn influenced by rates of settlement and mortality. The shape and skewness of size-frequency distribution curves reflects recruitment, growth and survivorship versus mortality; species origination rates versus longevity.

The size-frequency distribution of colonies within a coral population is normally highly positively skewed (right-tailed), dominated by the smallest size classes (Bak and Meesters 1999; Bak and Meesters 1998). Abundance of juvenile colonies then commonly decreases exponentially with increasing colony size (Glassom and Chadwick 2006). Larger corals normally become steadily rarer in population size frequency distributions, but generally have decreased probability of mortality (total colony mortality rates) than smaller colonies, which are more vulnerable to factors causing tissue death than larger colonies (Hughes and Jackson 1985; Soong and Lang 1992). Certain exceptions to this rule have been recorded in reefs with high coral cover. For example, reefs dominated by fast growing tabular *Acropora* colonies may have limited space for settlement and survival of recruits, reducing the abundance and relative numerical dominance of juvenile colonies (Done and Potts 1992; Bak and Meesters 1999).

Scleractinian competitive and regenerative abilities generally also increase with colony size (Hughes and Jackson 1985; Soong 1993). Studies of foliaceous corals in the Caribbean showed the frequency of partial and whole-colony mortality to be higher among small corals, decreasing steadily as colonies got larger. Larger corals

experiencing partial-colony mortality also lost proportionally less tissue than smaller colonies (Hughes and Jackson 1985). Consequently, competition and other disturbances often result in total mortality of small colonies, whereas larger colonies have a higher chance of survival but may suffer substantial tissue loss (Soong 1993).

2.4.1 Effects of environmental disturbance on coral demography

Analysis of coral size-frequency distributions must take into account the environmental setting of the population in question. Individuals of a population exposed to a high-energy wave-exposed environment would naturally exhibit different population size structure than individuals in a more benign location (Karisa et al. 2008).

For example, the maximum size of *Acropora* colonies on an exposed reef crest will inevitably be constrained by breakage of larger colonies by turbulent conditions, whereas the same species might grow in much larger plating growth forms in calmer conditions. As such, differences within any one taxon with a broad environmental tolerance range may reflect varying degrees of environmental disturbance or stress histories. In other words, the population structure or demography of a species in different habitats or depth zones may differ due to these natural environmental stressors.

While healthy populations of most scleractinia normally exhibit significantly positively-skewed size frequency distributions with populations dominated by smaller colonies, coral size frequency distribution is often strongly distorted by disturbance. Alterations in population structure may result from diverse factors including variations in adult fecundity, juvenile recruitment success, post settlement mortality or settlement site availability, all of which may change as environmental stressors increase (Bak and Meesters 1999). Thus, demographic structures are able to carry evidence of past disturbances. For example a population tilted towards larger size classes could indicate high fecundity, whereas size-frequency distributions skewed towards small size classes ('left skewed') might be indicative of high mortality in intermediate sizes, which could in turn represent a potential indicator of time-lag responses of coral populations to disturbance (Nystrom et al. 2008).

Studies from the Caribbean have shown corals to increase in mean size at impacted sites as a result of reduced recruitment and juvenile survivorship in turbid water (Bak and Meesters 1998). This is because in turbid environments sedimentation and poor water quality may inhibit settlement or survival of juveniles, reducing some of the recruit cohort and driving a more centralised colony distribution (Meesters et al. 2001). Colonies in such a case may thus be fewer, but larger.

Differences in size frequency distributions between neighbouring sub-populations of the same species at reefs at Curaçao have been attributed to environmental, rather than genetic, differences between sub-populations (Bak and Meesters 1999). Studies of coral populations in Curaçao and the Florida Reef Tract concluded that disturbance limits the abundance of small corals, causing a relative increase in the abundance of large colonies and an under-representation of small colonies (Bak and Meesters 1999). The latter authors hypothesise that coral populations become increasingly negatively skewed (i.e. showing relatively higher abundance of larger colony sizes) in response to ongoing environmental stress and disturbance, with relatively higher mortality of recruits and juvenile size classes of corals, and lower variation in size frequency distribution of corals. These hypotheses indicate less recruitment in disturbed populations, with populations aging without replenishment. These authors emphasise the need for testing these hypotheses through monitoring of size-frequency distributions in degraded environments (Bak and Meesters 1999).

Modelling the effects of increased temperature on populations of three pocilloporids on the Great Barrier Reef supported this hypothesis by indicating that sub-lethal temperature increases will increase the relative abundance of large colonies of all three species at the expense of smaller colonies (Edmunds 2005). This model did not incorporate effects of temperature on recruitment or mortality, so the results should be interpreted with caution, however it is supported by studies of mortality rates during the 1982 mass bleaching event on the Great Barrier Reef which showed an inverse relationship between mortality rates and colony size across four families of coral, consistent with other studies of coral survivorship (Connell et al. 1997).

Interpretation is complicated by the fact that a number of studies show contrasting impacts of disturbances on coral population distributions, where corals in a population are smaller after bleaching at sites exposed to chronic anthropogenic disturbance. In these cases, small and juvenile colonies have been recorded to show better survival than large mature colonies at some reef sites (Loya et al. 2001; Riegl 2002; McClanahan et al. 2008).

For example, surveys in Kenya have shown that coral bleaching resulted in dominance of small-sized colonies in most taxa. For most taxa studied, mean coral size and size frequency distribution were influenced by fishing pressure and bleaching stress, resulting in generally reduced colony size and reduced skewness of populations (McClanahan et al. 2008). The right-tailed skews in colony size frequency distributions were significantly reduced in *Acropora*, *Hydnophora* and *Montipora* following the 1998 mortality event (McClanahan et al. 2008). *Astreopora*, *Goniopora*, *Hydnophora*, *Acropora*, *Alveopora*, *Cyphastrea*, *Favia*, *Favites*, *Montipora*, *Pocillopora*, *Galaxea*, *Pavona*, *Platygyra*, branching and massive *Porites* and *Synarea* showed significant changes in size structure at protected reefs before versus after 1998. *Stylophora* and branching *Porites* were the only taxon that changed its size structure at unprotected reefs. Notably, *Fungia* did not experience decreases in size, abundance or size distribution as a result of bleaching or fishing disturbance (McClanahan et al. 2008).

This research also showed that the relative proportion of large corals increases with protection; a higher relative proportion of the largest size classes was recorded in sites that had been protected for longer periods. Studies of colony size distributions across 26 taxa at 7 lagoonal reef sites showed that many genera exhibited statistically larger mean colony sizes at protected reefs compared to unprotected sites. Only *Pavona* showed larger colonies at unprotected sites (McClanahan et al. 2008).

2.4.2 Impacts of hard coral demographic changes on population replenishment

Stress-mediated perturbations to size frequency distributions have serious implications for reef health, since colony size influences fecundity, mortality, and other life-history traits (Edmunds 2005).

Just as differential coral mortality between species reduces the taxonomic diversity and functional redundancy of coral communities, differential mortality within species reduces genetic variability of populations. Thus if thermal and/or anthropogenic stress shift coral size frequency distribution in such a way as to favour juvenile and small colonies (as documented in McClanahan *et al.* 2008), the population will become genetically dominated by small colonies, with overall lower diversity of gametic output.

This shift towards smaller colonies might result in higher turnover, greater genetic diversity, decreased dominance of larval populations by few large colonies, and more rapid adaptation. However, larval output is proportional to colony size, since colony size reflects the number of sexually mature polyps in coral colonies, in turn determining colony fecundity.

Therefore loss of large old colonies from populations will have a seriously detrimental effect on population replenishment, since older corals are considerably more fecund than younger colonies. At its most extreme, a shift towards the smallest colony sizes would result in impaired population fecundity by the higher relative abundance of pre-reproductive colonies within populations (Done, 1999).

Importantly, variability in size frequency distributions may reflect greater phenotypic plasticity, and greater ability to respond to environmental stress (Bak and Meesters 1999). Thus whether disturbance favours a relative abundance of either large or small colonies, truncation of a population's size structure in favour of either larger or smaller colonies is likely to reduce the populations 'buffering capacity' to environmental disturbances, reducing the stability of population dynamics (Brander 2008).

2.4.3 Effects of partial mortality on population demography

Corals, being colonial, modular organisms, can suffer partial mortality that distorts the relationship between colony size and age. Coral populations normally comprise numerous cohorts of different ages (Hughes et al. 1999). Many common disturbances affecting corals have the effect of reducing the area of live coral tissue. Thus partial mortality is an important factor regulating colony size and overall colony fecundity.

Both fishing and bleaching cause partial as well as full coral mortality (Loya et al. 2001; Baird and Marshall 2002). Consequently bleaching and over-fishing act to break up as well as eliminate colonies, across taxa (McClanahan et al. 2008). Owing to the effects of partial mortality on colony growth, as well as the effects of colony fission and fusion, coral size and age are often poorly correlated. For example, partial mortality can cause one large colony to convert to several smaller size classes, while in the smallest size classes, it is more likely to result in total colony mortality. It is thus quite possible for an adult colony to shrink in size as a result of partial mortality and effectively be 'overtaken' by a younger juvenile. Studies have shown that partial mortality of colonies killed more coral tissue than did the mortality of entire colonies (Hughes and Jackson 1985). The latter also showed widespread temporal variability in coral tissue loss, both through partial and whole-colony mortality, indicating that colony growth is an erratic process, often interrupted or reversed by disturbances.

Size frequency distributions of foliaceous corals cannot be accurately used as a proxy for age structure because small colonies can be old due to partial mortality, fission and fusion (Hughes and Jackson 1985). Bak and Meesters (1998) argue that for submassive, massive, sturdy branched, and upright blade colonies studied, partial mortality, particularly below the modal size of a species, precludes interpolation of the age structure of the population from size frequency distribution data (Bak and Meesters 1998). Thus size is generally not regarded as an appropriate proxy for colony age (Soong 1993; Hughes and Jackson 1985), and population age distributions (or the number of colonies surviving through successive age classes) should be inferred from size-frequency data.

Accurate measurement of a coral population’s age structure would require monitoring the population throughout the corals’ life cycle; an impractical undertaking. Field surveys commonly depend therefore on estimating coral age by dividing colony diameter by the average annual linear extension rate, or by using colony size as a hypothetical proxy for colony age.

2.5 Overview of status of coral reefs in selected study regions

This study focused on coral reefs in four countries within the western Indian Ocean and Red Sea. In addition to having being exposed to different levels of thermal stress over the past 15 years, these reef regions were selected as being representative of varying degrees of chronic anthropogenic disturbance. Consequently, these sites provide valuable insight into the possible impacts of varying environmental disturbance on coral communities within this ocean.

Table 1 summarises the broad differences between these regions in terms of exposure to past climatic and anthropogenic disturbances.

Table 1. Relative severity of anthropogenic and thermal disturbances at survey regions since 1998

Country	Region	Fishing pressure	Pollution	Past mass mortality
Madagascar	Toliara	High	High runoff and fluvial sedimentation	No documented mortality since 2003, anecdotal evidence of severe mortality events in 1998 and 2002
	Andavadoaka	Variable, with management	Moderate organic runoff	No documented mortality since 2003, anecdotal evidence of severe mortality events in 1998 and 2002
Seychelles	Granitic islands	Variable, with management	Moderate	Severe mortality affecting all reefs 1998, subsequent bleaching in 2002 and 2003
Saudi Arabia	Farasan Banks	Low	Low	Unknown
British Indian Ocean Territory	Chagos archipelago	Negligible	Negligible	Severe mortality affecting all atolls in 1998, subsequent localised mortality episodes recorded in 2005

2.5.1 Chagos

Situated in the central Indian Ocean the Chagos archipelago has been largely uninhabited for approximately 35 years; four of its five islanded atolls remain uninhabited, while a military base exists on the southern atoll of Diego Garcia. The archipelago comprises a further 10 submerged atolls and banks, which spread across 100,000 km² of ocean. The archipelago plays a critical role in the ecological connectivity of Indian Ocean reef systems, acting as a biological 'stepping stone' on the south equatorial current, which carries larvae connecting the highly biodiverse waters of the southeast Asian archipelagos with those of East Africa and the western Indian Ocean region.

Chagos reefs suffered very heavy mortality of corals and soft corals to at least 30m depth following the severe coral bleaching event of 1998, related to anomalously high sea surface temperatures caused by the El Niño Southern Oscillation (ENSO) event (Sheppard 1999; Sheppard et al. 2002). Subsequent surveys showed that up to 100% of hard corals died at reef sites in all atolls studied, with shallow reefs particularly heavily impacted.

Whilst most other reef sites in the central and western Indian Ocean also experienced widespread bleaching as a result of this ENSO episode, the maximum depth of reef mortality in parts of the Chagos archipelago, particularly in central and southern atolls, extended deeper than most other locations in the region (Sheppard and Obura 2005). Heavy mortality reduced previously thriving reef habitats to vast expanses of bare limestone to at least 30 m depth in the southern atolls. This may have been a result of the exceptionally clear oceanic water in the isolated archipelago, which enabled greater penetration of incident light. This was exacerbated by a prolonged period of calm seas throughout the 1998 bleaching episode, which led to less surface reflection and greater penetration of light (Sheppard 2006). Repeated, though mostly less severe, bleaching events have been observed throughout the archipelago in the intervening years. This is in common with many other parts of the Indian Ocean.

Chagos reefs, amongst the remotest in the Indo-Pacific, are almost entirely free of direct anthropogenic impacts. With the exception of low levels of illegal fishing on

outer atolls and the effects of terrestrial military development on Diego Garcia whose impacts are very localized (Guitart et al. 2007), climatic change and broad-scale oceanic and meteorological disturbances currently represent the only serious threats to its coral reef health and ecosystem function.

Owing to its geographical isolation and current political status the Chagos archipelago provides an effective *de facto* marine reserve and a natural 'control' site for monitoring specific responses and recoveries of coral reefs to natural disturbances and climate-related mass mortality events in the absence of local human impacts.

2.5.2 Farasan Banks, Saudi Arabia

Situated in the central Red Sea, Saudi Arabia's Farasan Banks comprise a complex network of reefs and atoll structures across approximately 30000 km² of ocean, located between 7 and 100 km offshore. The Farasan Banks are contiguous with the more southerly Farasan Islands, and incorporate diverse habitat types, including deep water lagoons and ridge reefs, the latter a morphology distinct to the Red Sea created by an unusual flowage of Messinian evaporates. These structures are geomorphologically similar to atolls and typically exhibit dramatic vertical profiles with pronounced seaward drop-offs.

Red Sea coral reefs are of high global biogeographic importance, with approximately 10% species level endemism (Devantier et al. 2000). The central Red Sea, including the Farasan Banks, contains many species absent from the northern and southern Red Sea, and central Saudi Arabia's offshore reefs are thought to act as important regional stepping stones for gene flow within the southern Red Sea (Turak et al. 2007; DeVantier and Pilcher 2000).

Previous research in this region has been extremely limited, with no published studies carried out in recent decades. Almost nothing is known of the extent to which Farasan Banks reefs may have experienced thermal stress-related bleaching over the past decade – a time during which many Red Sea and Indian Ocean reefs have suffered serious degradation and mortality as a result of bleaching stress. Consequently, interpretation of potential climate-related disturbances that may have impacted the

Farasan Banks in the recent past depends on contemporary observations and interpretation of evidence of stresses that have impacted other coral reef systems in the southern Red Sea.

The Red Sea harbours relatively high levels of endemism of coral reef fauna, and is regarded as a separate Indopacific coral reef zoogeographic province or sub province (Sheppard et al. 1992; Devantier et al. 2000). Surveys undertaken north of the Farasan Banks along the central Saudi Arabian Red Sea coast between Jeddah and the Gulf of Aqaba in 1998 documented high ecological integrity of coral reefs across a large area. Reefs were characterised by highly diverse coral communities (around 260 species – at the time considered the highest scleractinian diversity in the Indian Ocean west of Indonesia) and a high ratio of living to dead coral cover (approximately 6:1) (Devantier et al. 2000). It is thought that the low levels of human impact have afforded the region a degree of ‘insularity’ avoiding the degradation experienced in most other areas of the Indopacific (Devantier et al. 2000).

Past surveys carried out south of the Farasan Banks in the Yemeni Red Sea have suggested that coral populations in the region are acclimated to the extremely high sea temperatures and above-average salinities typical in the region. These temperatures, with an annual average of 31°C, and maximum of 38°C, would typically kill conspecifics in other regions, and as a result local populations are thought to have adapted to tolerate thermal stress. It has been suggested that the southern Red Sea may contain reefs that will survive warming and acidification the longest (Veron et al. 2009), but it remains unclear whether southern Red Sea corals will in fact harbour greater resilience or vulnerability to global climate change.

Notwithstanding the healthy condition of these reefs, and the likely adaptation of their corals to higher temperatures than many other Indopacific reefs, extensive bleaching and subsequent mortality of coral reefs were also recorded in the Yemeni coast of the southern Red Sea in 1998 (Pilcher and Alsuhaibany 2000).

Bleaching affected many genera of scleractinia, alcyonaria and *Millepora* spp., and was most severe in shallow waters <6m depth. Bleaching followed anomalously warm sea

surface temperatures for more than one month preceding August, although reef areas adjacent to known cool water upwelling, such as those in the Gulf of Aqaba and Al-Wajh Bank, were little affected (DeVantier et al. 2004).

Reef development in the Yemeni Red Sea is lower than the central and northern Red Sea, in part because of the region's comparatively wide shallow coastal shelf, soft substrata, and highly sedimentary nature. High diversity communities are generally characteristic of clear-water offshore seaward reefs and submerged patches or pinnacles, whereas low diversity reefs are more typical of shallow and turbid reef environments, with lower hard substrate and hard coral cover, and higher rubble and calcareous encrusting algal cover.

Similar inshore/offshore gradients of reef health have been recorded further north at the Farasan Islands (contiguous with the more northerly Farasan Banks) where coral cover has been shown to increase with distance from the mainland, and the proportion of dead coral declines with distance from the mainland (Al-Yami and Roupheal 2000).

Yemeni reefs have also shown signs of recent mortality, attributed to coral bleaching and *Acanthaster planci* predation, with dead coral cover exceeding live coral cover, and providing a favourable habitat to macroalgal growth and bio-eroding species. Across all sites, live hard coral, dead hard coral and macroalgal coverage averaged 11%, 29% and 21% respectively (Turak et al. 2007). Extensive recent mortality of large (>4m diameter) *Acropora* colonies, attributed to *Acanthaster planci* predation, occurred from 8-20m depth (Turak et al. 2007).

2.5.3 Granitic Seychelles

The inner Granitic Seychelles islands lie in the centre of the Seychelles Bank. The Seychelles Bank is an oceanographically remote, shallow carbonate platform, 40-60 m in depth, located at the northern limit of the Mascarene Ridge; the largest emergent submarine structure in the western Indian Ocean (Badyukov et al. 1989).

The islands' reefs suffered massive mortality in 1998, with subsequent bleaching events occurring in both 2002 and 2003. Juvenile and recently-recruited corals were

most heavily impacted during the 2002 bleaching event (Engelhardt 2004). Fishing effort on Granitic Seychelles reefs has remained relatively constant since the early 1990s, and with the exception of isolated occurrences of chronic sedimentation and pollution, the region's reefs are considered to be largely unaffected by anthropogenic disturbance.

Surveys conducted in 2005 showed that, relative to their pre-1998 condition, the reefs had lost much of their coral cover and structural complexity. The reefs also showed a 7-fold increase in macroalgal cover and an increasing relative abundance of encrusting and massive corals compared to the previously dominant branching habitat-forming taxa (Graham et al. 2006).

2.5.4 Madagascar

Madagascar's coasts span 14° of latitude, harbouring over 3500km of coral reefs in widely differing oceanographic settings. The most extensive reefs are found in the northeast, northwest, and in the southwest of the country, and together support the highest species richness of corals in the central and western Indian Ocean (Veron and Turak 2005).

All of the country's accessible reefs are exploited by traditional artisanal fisheries. Fishing effort on reefs has increased considerably over the past decade as a result of rapidly expanding market demand from fisheries collection enterprises. The growth of fishing effort has coincided with diversification of the range of species targeted by fishers and collectors.

In addition to the impacts caused by unsustainable fisheries, which are largely unmonitored throughout Madagascar, reef degradation also occurs from chronic anthropogenic impacts of high sedimentation from fluvial discharge, organic enrichment and pollution of coastal waters. Cyclonic activity in Madagascar is also high, causing severe localised damage to coral reefs approximately annually.

Degradation of Madagascar's coral reefs over the past decade may also be attributed in large part to the bleaching-related mass mortality events of 1998-2002, as monitored

and quantified on coral reefs throughout other central and western Indian Ocean regions over recent years (Goldberg and Wilkinson 2004). Bleaching events are thought to have caused high mortality to many of Madagascar's reefs in 1998, 2001 and 2002, although no quantitative data exist to document the extent or nature of these mortality episodes, or the responses of coral reefs in the immediate aftermath.

The occurrence of strong bleaching events in the southwest in 2001 and 2002 are supported by high degree heating week (DHW) values for this region; south-western reefs have experienced higher cumulative degree heating weeks than other areas of Madagascar during recent sea warming episodes (McClanahan et al. 2009). It is likely that fast growing corals, in particular *Acropora*, were particularly heavily impacted by these bleaching events, as was observed at numerous monitoring sites elsewhere in the Indo-Pacific (Sheppard et al. 2002; Wilkinson 2002; McClanahan et al. 2004). Notwithstanding a moderate bleaching episode affecting northeastern reefs in 2005, no subsequent widespread bleaching-related coral mortality events have been recorded in Madagascar over the past 6 years.

Coral reefs run continuously for over 450km along Madagascar's southwestern coastline, over 3 degrees of latitude. Two survey regions are examined within this reef system; Toliara's *Grand Récif* and Andavadoaka. The southwest reefs are considered to be amongst the country's most degraded coral habitats, with more erect algae cover and lower coral cover than north-western and eastern reefs (McClanahan et al. 2009).

The central geographical feature of this predominantly fringing reef system is the geomorphologically distinct *Grand Récif*, a barrier reef that lies adjacent to the regional capital city Toliara. The *Grand Récif* is 19 km in length, with a shallow reef area of approximately 33 km², lying between 1.5 km and 12 km offshore, directly seaward of the coastal city. The city's port lies protected within the reef's lagoon, less than 2 km from the back-reef slope.

Toliara's *Grand Récif* was the focus of a number of studies in the 1960s and 1970s, which provide valuable insight into the condition of the region's coral reefs prior to contemporary high levels of direct anthropogenic disturbance (Pichon 1971; Pichon,

1978). Apart from a limited number of fisheries-related studies from the late 1990s, there has been scant published research documenting the status of Madagascar's coral reefs since then (Laroche and Ramananarivo, 1995; Laroche et al. 1997).

The city's population has increased by 53% in the 15 years between 1993 and 2008 (INSTAT 2007). Population growth coincided with an increase in artisanal fishing pressure on the city's adjacent reefs. Mangrove stands once lining the shoreline between the city and the *Grand Récif's* lagoon have been almost entirely removed in recent decades. There is no centralised organic waste disposal system for the region, and human waste is commonly disposed of on the deforested mudflats for removal by each outgoing tide. Lagoonal water is highly turbid, and there are no management controls in place regulating artisanal fisheries, pollution or waste disposal. Those environmental regulations that do exist are rarely implemented due to a lack of enforcement capacity by relevant authorities (Harris et al., 2010).

The remote region of Andavadoaka lies at the northern limit of Madagascar's emergent southwestern reef system, approximately 200km north of Toliara. This region comprises near shore and offshore fringing reefs as well as a number of distinct lagoonal patch reefs, and has become a nationally important site for applied marine research, with a number of ecological and biodiversity studies undertaken in recent years to support ongoing marine and coastal conservation efforts in the region (Gillibrand et al. 2007; Nadon et al. 2007; Harding et al. 2006; Harris 2007).

Like Toliara, Andavadoaka's reefs are chronically disturbed, experiencing high levels of fishing effort from subsistence and artisanal fishers. However these reefs are not exposed to the levels of organic runoff and pollution that are seen in Toliara, and are generally considered to be representative of the healthiest reef communities in southwest Madagascar (Nadon et al. 2007). A number of sites within the region are subject to effective no-take management controls as part of the Velondriake Locally-Managed Marine Area (LMMA)(Harris 2007).

2.6 Limitations of conventional methodologies for assessing reef benthic composition

Field methods for assessing coral reef benthic communities tend to focus on biodiversity and/or reef benthic composition, rarely investigating the aspects of size-frequency dynamics or population structures within and between coral communities that add greatly to understanding.

Common methods for assessing reef benthic composition typically measure simple parameters such as relative coverage of major benthic groups and substrate types. These measures generally provide only a crude measure of ecological condition. For example, the widely-used intercept transect method assumes a reef to be a 2-dimensional habitat, giving little indication of reef rugosity. Moreover, information on coral community composition or population structure is rarely captured using this approach.

Many studies use coral cover as a proxy for reef health, assuming that high coral cover generally relates to good reef health. However, such inferences of reef health may be extremely misleading. For example, a return of coral cover following a disturbance episode to pre-disturbance levels is usually considered to equate to recovery of the reef community to its previous condition. Yet this supposes that reefs with high coral cover are more 'healthy' than those with low coral cover, and fails to take into account both the natural spatial gradient of coral abundance that exists on reefs, and processes of succession. Large reef tracts typically show considerable variability in cover of stony and soft corals in response to site-specific characteristics (Devantier et al. 2000). Indeed, such natural variability is indicative of a healthy system, and should not be assumed to be indicative of differential levels of ecological health or disturbance.

Moreover, studies have shown that apparent recovery of coral cover can occur without recovery of community structure (Berumen and Pratchett 2006). Ecologically-important differences may exist between two coral communities with the same overall coral cover. For instance, the two communities might support different age structures of populations, with one community comprising a small number of large, structurally-complex colonies, and the other community being made up of a large number of

juvenile forms that have not yet made a significant contribution to reef architectural complexity. Benthic composition transects commonly overlook this 'maturity discrepancy'; a potentially serious limitation given that recovery of absolute coral cover may precede recovery of rugosity and complexity by 10-20 years (Sheppard et al. 2008).

2.6.1 Challenges of surveying coral communities

Many problems commonly encountered when surveying coral communities are associated with monitoring the smallest cohorts within coral assemblages, particularly the youngest, newly-metamorphosed coral recruits.

The challenge when incorporating very young colonies (which add almost nothing to total coral cover at this stage) is to obtain data that may be considered broadly representative of the overall juvenile coral community within a given reef area. Recruitment success of corals is non-random, and may be influenced by a range of environmental factors including depth and substrate type, orientation and morphology (Norstrom et al. 2007; Bak and Engel 1979; Mundy and Babcock 1998). Moreover, there can be great inter-annual variability in settlement rates (Wallace 1985).

Young corals, typically 1 – 2 mm in diameter, normally remain cryptic, commonly settled in reef crevices or cracks, or hidden by larger epibenthic organisms, until they have attained a clearly visible size (Bak and Engel 1979). This results in under-surveying of small juveniles in most visual surveys and a lag period of potentially up to 1-2 years occurring between larval settlement and the point at which corals can be accurately and reliably recorded by visual census. Photoquadrats, taken vertically, are unable to accurately record new corals < 1 – 2 cm in diameter, and likewise do not detect corals situated in a non-horizontal plane of orientation on the reef (Edmunds et al. 1998). Even larger colonies are often misidentified, or simply remain unseen, when surveyed retrospectively by photoquadrats, as a result of colony crypsis and difficulties of identification from 2-dimensional images.

These limitations to sampling often prohibit monitoring of newly-metamorphosed recruits *in situ*, and mean that important growth and life history processes may be

omitted from field surveys. Thus, sampling strategies for studies of juvenile corals vary greatly between studies. Some studies sample only areas of substrate deemed suitable for the settlement of coral larvae (normally bare rock or carbonate surfaces free from macro-algae, live hard and soft coral, sessile invertebrates and excessive sediment). Other approaches sample juvenile corals randomly across all reef substrata.

In addition to the challenges associated with monitoring newly-recruited corals, sampling larger colonies also poses significant difficulties, in large part because of the considerable variation in colony sizes both within and between taxa. Differences in colony size, growth, longevity and partial mortality can all prevent useful comparison of size structures and distributions between populations of different species and/or genera.

Because colony growth for perhaps most species therefore rarely follows a linear pattern with coral age, in some cases, size increases more rapidly the larger the colony, while some, such as tabular and ramose *Acropora* spp. are encrusting for a few years before commencing vertical growth. Similarly, a loss of colony diameter through partial coral mortality of, for example, 3 cm, would have a profound impact on a small juvenile colony but a far less significant biological impact on a large adult colony.

Many species vary enormously in growth form. Morphological plasticity is such that the same species may exhibit different growth forms in different biotopes, or display different genotypic morphotypes. Both these factors can show substantial geographic variation (Devantier et al. 2000). Corals also vary considerably in size both within and between species, some attaining several metres in diameter, having grown from a newly settled polyp of only 1-2 mm in size. While some species grow to over 100,000 cm², coral populations are invariably numerically dominated by small area classes (Soong 1993). These characteristics of coral populations present analytical problems for studies comparing area frequency distributions of species on a linear scale, since any particular increase in colony area will have a vastly different relative effect on overall colony area for a newly recruited juvenile than for a large coral (Vermeij and Bak 2003).

Of the few studies that have investigated population structures of Indopacific hard corals in recent years, sampling approaches have tended to group corals into size-class categories (Devantier et al. 2000; Obura 2009). Although this provides a means of obtaining a broad understanding of approximate population structures, size categories are generally classified widely, at a resolution that prevents discrimination of changes and dynamics between the smaller juvenile, vulnerable size stages.

These factors are important to understanding reef community dynamics, especially in the context of recovery from the massive 1998 mortality in the Indian Ocean. The methods and measurements used here attempt to capture this information which, in most studies, has been omitted.

METHODS AND MATERIALS

3 Site selection and sampling

Field research was carried out between 2006 and 2009 in the Chagos archipelago, the Seychelles, Madagascar and Saudi Arabia. These locations reflect different levels of anthropogenic disturbance, latitude and biogeography as well as different temperature environments, particularly in terms of variation of mean temperatures, exposure to past bleaching-related mortality and possible acclimation to temperature.

These differences are expected to have affected the abilities of corals to adapt to thermal stress events (Ateweberhan and McClanahan 2010, in press). Differing responses of coral communities between reefs are, in turn, likely to affect reef resilience to anthropogenic as well as ongoing climatic disturbance.

It is hypothesised that over recent years physical and temperature differences have resulted in differing reef composition between regions. Such differences are anticipated both at the macro level of the structure and composition of the entire reef community, as well as more specifically within the communities and populations of scleractinia.

Within each region, surveys were carried out at a number of sites considered to be representative of a range of reef conditions. Surveying was not focused on sites considered to be either particularly 'healthy' or degraded, but aimed to cover an objective, representative range of sites in each region. Replicate sample numbers differed between regions as a consequence of survey programmes. A total of 108 reef sites was examined in the Indian Ocean. Sites were located in the following areas within the 5 survey regions (Figure 3):

Chagos

Surveys were carried out between February and March 2006 at 19 sites in 5 atolls of the archipelago. From north to south the atolls visited were (with numbers of survey sites in brackets): Peros Banos (4), Salomon (5), Great Chagos Bank (3), Egmont (2) and Diego Garcia (5) (figure 1).

Granitic Seychelles

Surveys were carried out at 20 sites in 7 survey areas around the islands of Mahe and Praslin in the Granitic Seychelles in April 2008. With the exception of one survey area, three sites were surveyed within each area. Following the sites and categorisation of Jennings (1996), reefs were classified as either 'patch', 'carbonate', and 'granite', with one of each reef type represented at each area. 2 survey areas (comprising a total of 6 sites) are managed as no-take marine reserves: St Anne Island at Mahe; and Cousin island at Praslin.

Madagascar - Andavadoaka

Surveys were carried out at 14 sites in Andavadoaka, southern Madagascar, between June and August 2008. Sites were distributed across three geomorphological reef types within the region: near shore fringing reefs, offshore fringing reefs, and lagoonal patch reefs following the geomorphological categorisation of reef types by Nadon *et al.* (2007) and Gillibrand & Harris (2007). At the time of surveying, none of these sites were protected from any form of fisheries gear restrictions or management, although 3 lagoonal patch sites experienced *de facto* protection on account of their remote location and relatively lower fishing effort.

Madagascar – Toliara

Surveys were carried out at 4 sites on the outer reef slope of the *Grand Récif* barrier reef adjacent to the city of Toliara in southwestern Madagascar in July 2008. Sites were selected to be as close as possible to those examined and described in detail by Pichon (1978)(Mara, 2008, pers. comm.).

Southern Red Sea - Farasan Banks, Saudi Arabia

Surveys were carried out at 52 reef sites across the Farasan Banks, southern Saudi Arabia, from a total of 58 sites visited by the Living Oceans Foundation expedition in April 2009.

3.1 Additional data incorporated in analysis

Additional comparative data were obtained from studies carried out by the Kenya-based marine research organisation CORDIO as part of the IUCN-funded Climate Change and Coral Reefs (CCCR) reef resilience assessment programme. These studies, undertaken at a number of coral reef regions throughout the Indian Ocean from 2007 until 2010 employed a method assessing hard coral community composition whose results are comparable to those generated from the approaches used here (section 4.5; page 64). Data provided by the CCCR programme were collected in the following sites (surveyor in parenthesis) within each survey region (Figure 1; Table 3):

Seychelles (Obura, D., 2008)

10 sites around Alphonse Island in the Amirantes Group, in April 2008.

Madagascar (Obura, D., 2008)

16 sites within the Nosy Hara marine protected area, northwest Madagascar, as part of a WWF-funded coral reef assessment expedition in December 2008.

Saudi Arabia (Obura, D., 2008)

33 reef sites in the region of Al Wajh and Yanbu during a Living Oceans Foundation research expedition in April 2008.

4 Research methodology

The methodologies used in this research sought to overcome several limitations of standard benthic composition and coral reef community assessments (English et al. 1997; McClanahan 2008), by collecting detailed data of coral community composition and population structure. Since these parameters vary as a function of depth, the depth range of the study was fixed at 10 m for all field surveys carried out in this research. At Chagos only, juvenile colony surveys were repeated at 25 m, 15 m and 5 m depth. Comparative CCCR data were generally collected within a broader depth range of 7 m – 13 m.

4.1 Adult colonies

The genus and longest diametric axis (cm) were recorded from all hard corals >10 cm lying within a randomly-placed 10 m x 1 m belt at 10 m depth. Transects were laid along a contour at 10 m depth at points of the reef selected as being heterogeneous and accurately representative of the reef community at the 10 m depth contour of the reef site.

The largest diameter of each colony was measured with vernier callipers, measuring tape or ruler *in situ* over the surface of the colony (Bak and Engel 1979). Only colonies lying with more than 50% of colony surface area within the 10 m² belt transect were measured. Up to 16 replicate transects were sampled per site.

4.2 Juvenile colonies

Juvenile corals were identified and counted by recording size and genus *in situ* of all juvenile hard corals (≤ 10 cm diameter) found within randomly-placed 0.11 m² (33 cm x 33 cm) quadrats. This small quadrat size was chosen since recruitment estimates generated by studies using large quadrats (1 m²) greatly under-sample true juvenile coral abundance (Miller et al. 2000)

Up to 170 replicate 0.11 m² quadrats were sampled per site within the same reef area covered by the belt transects, again at 10 m depth. This direct examination of juvenile corals on the substratum is favoured above photographic methods of coral identification because of crypsis of juvenile colonies (Edmunds et al. 1998).



Figure 1. Location of eight survey regions within the central and western Indian Ocean

Small and cryptic juvenile colonies are commonly difficult to identify to genus level (Glassom and Chadwick 2006). Where genus could not be accurately identified, colonies were either recorded to family level or simply noted as 'unknown'. Mobile coral ramets that were clearly the product of fragmentation of older colonies were omitted from the census.

4.3 Calculation of surface area

For both adults and juveniles colony surface area was modelled as approximately equivalent to πr^2 , r being half the maximum diametric axis measured for each colony. For conical-shaped massive colonies, with a raised central feature, r was measured directly along the colony from the central point, rather than from above as an 'aerial footprint' measurement. For overhanging, plate or table colonies, only the upper surface of corals was measured.

Although other sampling methods enable more accurate calculation of colony surface area (such as measuring colony height and perpendicular diameters in addition to the colony's longest axis (Fisher et al. 2007; Crabbe 2009), or taking account of partial mortality to approximate the proportion of live tissue within a colony), such approaches were not adopted in this study. Given the limited time in most areas visited, it was considered favourable to capture as large a sample size of colonies as possible, with each colony's surface area being based on a single 2-dimensional diametric measurement.

The surface area data obtained therefore represent a simplification of colony shape and morphology, which is based on the assumption that, across all colonies of any particular taxon, the 'average' colony surface area is approximately equal to the surface area of a flat or uniformly centrally-domed circular colony. For a small number of uncommon taxa - such as certain fungiid genera whose colonies are never circular - this assumption is clearly invalid, and therefore limits the inferences that can be drawn from surface area data obtained from these taxa.

4.4 Sampling

Figure 2 summarises the sampling strategy and the nesting of quadrats, transects and sites within each survey region visited. Up to 16 randomly-placed 10 m transects were sampled within each site. Up to 170 randomly-placed 0.11 m² quadrats were sampled within the reef areas sampled by the transects within each site.

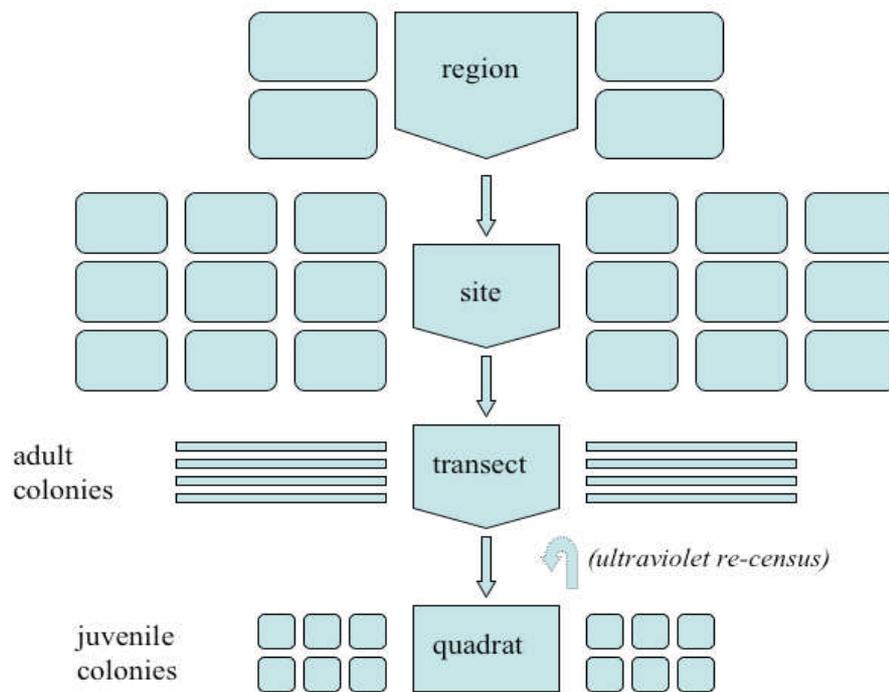


Figure 2. Sampling design of adult and juvenile coral surveys, showing the nested sampling design of quadrats within transect areas, within survey sites, within each survey region

4.5 Differences between coral sampling in CCCR methods and this study

The CCCR methodology used by collaborators to collect comparative data from the three additional survey regions differs from that employed in this study in four areas:

- (i) It uses generally longer transects of variable length (depending on survey time available, up to 25 m x 1 m, rather than the fixed 10 m by 1 m belt used in this study) and larger quadrats (1 m x 1 m rather than the 0.33 m x 0.33 m quadrat used in this study).
- (ii) It groups colonies into one of 9 discrete size bins (0-2.5 cm, 3-5 cm, 6-10 cm for juveniles; 11-20 cm, 21-40 cm, 41-80 cm, 81-160 cm, 161-320 cm and > 320 cm for adults).

- (iii) It records only those genera considered *a priori* to be the most abundant within each survey region, and representative of a range of levels of susceptibility to bleaching (Obura and Grimsditch 2008).
- (iv) The depths of the surveys were variable, depending on the reef site.

In order to compare data collected during this study with those from CCCR surveys, data from the different studies were standardised (selected variables – taxon and/or size class - per unit area) where possible to account for differences between the two sampling approaches. Where standardisation of data was not possible, the likely implications of these differences in the resulting data are considered.

4.6 Ultraviolet surveying of juvenile colonies

Newly metamorphosed polyps are generally not possible to detect in field conditions until they have grown to several mm in diameter. Standard daytime ‘white light’ census carried out by conventional visual survey methods often fails to detect coral recruits until a minimum size has been reached, by which time a recruit may be over one year old (Wallace and Bull 1981). Even young corals several millimetres in diameter may remain undetectable to the naked eye, particularly in high relief habitats, so results are likely to under-report newly-metamorphosed coral recruits. This limitation in methodological accuracy prohibits investigation of community structure and population dynamics of the youngest coral recruits.

Juvenile coral tissues contain a high abundance of fluorescent pigments which emit wavelengths of light from blue-green to orange when illuminated by ultraviolet, blue or green light (Baird et al. 2006; Piniak et al. 2005) so that when fluorescent taxa are common, the fluorescence census techniques can greatly increase the counts of coral recruits (Baird et al. 2006). Therefore for surveying juvenile corals at all survey sites in the Farasan Banks, Saudi Arabia, daytime fluorescence censuses, using a blue light mask filter and the *NightSea FL5000 Flash Light*, were carried out. After using the conventional quadrat sampling methodology, each quadrat was subsequently resurveyed with the UV lamp, to highlight the location of small and cryptic colonies that might otherwise remain undetected. Data were recorded separately for all Farasan Banks sites, enabling comparison of the resolution of the two methods.

4.7 Taxonomic resolution

Corals were identified to genus level only in order to ensure taxonomic consistency. Analytical testing was carried out on both genus and family-level data.

4.7.1 Additional surveys

At several of the reef regions coral surveys were complemented by a number of additional biophysical assessments of the reef benthic community, described below. Not all methods could be employed at all survey regions (Table 2).

Table 2. Surveys undertaken by the author and collaborators during this study. Studies not carried out directly by the author are indicated, collaborators listed in italics.

Method	Chagos (2006)	Granitic Seychelles (2008)	Southwest Madagascar-Andavadoaka (2008)	Southwest Madagascar - Toliara (2008)	Saudi Arabia - Farasan Banks (2009)
No. survey sites	19	20	14	4	52
Juvenile coral surveys (10m)	✓	✓	✗	✗	✓
Juvenile coral surveys (variable depth)	✓	✗	✗	✗	✗
Adult coral surveys (10m)	✗	✓	✓	✓	✓
Benthic composition assessments	✓ PIT	✓ LIT and visual (<i>Wilson 2008</i>)	✗	✗	✓ Visual (<i>Rouphael 2009</i>)
Rugosity assessments	✗	✓ (<i>Wilson 2008</i>)	✗	✗	✗
Juvenile coral surveys (UV)	✗	✗	✗	✗	✓

4.8 Benthic composition

In the Granitic Seychelles, replicate intercept transects were carried out by the accompanying dive buddy to record the overall biotic cover on the substrate. The line intercept transect (LIT) (English et al. 1997) was used to allow rapid assessment of the composition of target benthic and substrate groups, identifying taxa within the benthos to genus level. LIT transects were supported by visual estimates of benthic cover, based on the surveyor's plan view of the benthos over the same survey area. This involved the diver hovering 1-2 m above the benthos and estimating percentage cover of massive, branching and soft corals, macroalgae, rubble and rock based on a visual

appraisal of the survey area (Wilson et al. 2007). The same method of estimating benthic cover was also applied at the Farasan Banks.

4.9 Reef rugosity

In the Granitic Seychelles visual assessment of habitat complexity was carried out by assigning each reef site a grading from 0 to 5, where 0 = no vertical relief, 1 = low and sparse relief, 2 = low but widespread relief, 3 = moderately complex, 4 = very complex with numerous fissures and caves, and 5 = exceptionally complex with numerous caves and overhangs (Polunin and Roberts 1993).

Table 3. Comparative surveys undertaken by collaborators, data contributed for analysis during this study

Method	Saudi Arabia Al Wadj (<i>Obura 2008</i>)	Northwest Madagascar (<i>Obura 2008</i>)	Alphonse/Desroches, Amirantes Seychelles (<i>Obura 2008</i>)
No. survey sites	33	10	16
Coral community surveys (CCCR methodology)	✓	✓	✓

4.10 Sea Surface Temperature (SST) analysis

Monthly mean SST data were obtained from the Hadley Centre Sea Surface Temperature 1 (HadISST1) dataset, from 1900 to 2009 inclusive, for each of the survey regions visited in this research, and comparative regions (CCCR data), to enable analysis of between-region spatio-temporal variability. HADISST1 data have high accuracy but low spatial resolution, limited to 1° x 1° latitude-longitude (Rayner et al. 2000) (<http://hadobs.metoffice.com/hadisst/>).

5 Analyses

Given the large size-frequency-by-taxa-by-samples data matrices created during this study, analysis firstly focused on reducing the complexity of data arrays through graphical representation of samples, as well as multivariate testing to identify and characterise statistically significant differences in community composition and population structure at different spatial scales, between sites and regions. Univariate and multivariate statistical analyses were carried out using PASW 18.0 (SPSS Inc.), Minitab 14.20 (Minitab Inc.) and Primer 6.1 (Primer-E Ltd.).

5.1 Graphical representations of data

Size frequency distributions, based on both the numerical abundance and total surface area of colonies, were calculated for juvenile (<100mm) and adult (>100mm) corals to examine life history and growth patterns exhibited by different populations and communities.

The proportion of total cover of the hard coral community in each region made up by juvenile corals and other size cohorts was examined by plotting the cumulative percentage of total coral abundance and surface area against colony size (Hughes and Jackson 1985). Size frequency distributions were also calculated based on the 9 CCCR colony size categories, for colony abundance and total surface area data, to enable comparison against data from CCCR survey regions. These size frequency distribution plots were repeated both with pooled data (all taxa), and individually across the most abundant taxa, to determine the composition of dominant genera and families to observed pooled community size frequency distributions. All plots were repeated to represent colony size frequency distributions in both absolute and relative terms.

Juvenile colony abundance data were plotted against benthic composition variables for data from the Granitic Seychelles and the Farasan Banks, Saudi Arabia. Pearson correlation analysis was used to determine whether significant relationships existed between juvenile abundance and benthic composition across all individual sites in each of these survey regions. Correlations were calculated separately for these two regions, in view of the different benthic assessment methods used in each region (Table 2).

5.2 Genus population distribution parameters

Within each region, colony size frequency data from all sites were pooled for each taxon to provide as a large a sample of each population as possible within each region (i.e. across all sites surveyed). This enabled analysis of differences in population structures between genera and between regions.

Area frequency distributions of coral populations are always skewed with large numbers of small colonies and progressively fewer larger colonies, the upper limit restricted by colony mortality. Natural logarithms of coral size frequency data can be

used to convert asymmetric distributions to normal distributions, enabling more direct interspecific comparison of the nature of frequency distributions (Bak and Meesters 1999). Log colony area distributions were therefore calculated to reduce right skewness in area-frequency distributions and to stabilise the variance, thereby reducing both non-normality and heteroscedasticity, as the basis for comparing populations within and between regions (Bak and Meesters 1998).

A number of frequency distribution parameters were then calculated from transformed data to compare population structures between taxa and regions. These included mean area, standard deviation, standard error about the mean, kurtosis and skewness (Meesters et al. 2001; Sokal and Rohlf 1995)(Appendix III).

The skewness of populations of corals from each region was calculated for every genus to depict the symmetry of population distributions, quantifying the relationship of small to large cohorts within each population. Normal symmetrically distributed populations have a skewness co-efficient of zero. Negative skewness values indicate left-skewed populations (i.e. populations with more small colonies than in a normal distribution), whereas a positive skewness indicates that more of the population appears to the high end - or the right - of a size frequency distribution plot. Kurtosis coefficients provide an indication of the flatness of the population distribution. Negative kurtosis values indicate populations with a flatter frequency distribution than a normally distributed bell-shaped curve, and vice versa.

Populations of each genus were compared between and within regions using One-Way ANOVA. Populations showing significant ANOVA test results were identified using the Tukey post-hoc multiple comparison test in Minitab 14.20. Prior to any parametric statistical analysis data were tested for normality using the Ryan-Joiner normality test function in Minitab 14.20. Populations displaying a departure from normal distribution were transformed using a Box-Cox transformation to ensure that data used in analyses met all assumptions of normal distribution (Box and Cox 1964). Power analyses were carried out on all data prior to parametric statistical analysis.

5.3 Multivariate analyses

Non-parametric and permutation-based approaches were adopted for both display and testing of multivariate data. Data were structured as matrices composed of samples (sites) by variables (taxa) and/or size frequency distributions.

5.3.1 Taxonomic composition of coral communities

Multivariate analyses were used to investigate the effect of various factors, both within and between reef regions. Factors tested included distance of reef sites from shore, latitude of site, orientation of site to prevailing swell (seaward/leeward), and region-specific factors including those used in past studies, such as the existence of management or reef geomorphology in the case of Andavadoaka, Madagascar and the Granitic Seychelles (Nadon et al. 2007; Jennings et al. 1996).

Analyses of differences in taxonomic composition of coral communities across all sites were carried out using non-metric Multi-Dimensional Scaling (MDS) ordinations based on Bray-Curtis dissimilarities of root transformed multivariate sample data. Genera and families (separately) were the variables used for taxonomic composition analysis. Square root transformation was used as a means of down-weighting the importance of highly abundant taxa (such as *Porites*) in the multivariate representations, so that community similarities depended not only on their values but also those of less common ('mid-range') taxa and rare corals. To examine the effect of transformation of data, all analyses were repeated with raw data (no transformation) and also compared with the most severe of transformations (conversion of data to presence/absence values only).

Analysis of similarities (ANOSIM) testing was used to identify significant differences between groups of samples defined by the above factors. ANOSIM was suitable on account of its lack of assumptions about the normality of the data or the variability of within-group replications, as well as its ability to analyse non-balanced designs (i.e. sites with unequal numbers of replicates, and regions with unequal numbers of sites). The variables (genera or families) that primarily accounted for Bray-Curtis dissimilarities between groups of samples were identified using the similarity percentages (SIMPER) routine (Clarke and Warwick 2001), to enable calculation of the

contribution of each variable to between sample similarities. Bubble plots were used as a means of superimposing taxon-specific variables of colony abundance and surface area over MDS ordinations of samples (Appendix I). For all multivariate analyses of trends in taxonomic composition across samples (reef sites and regions), testing was repeated with two sets of values calculated from the raw data:

- (i) colony density values, defined as the mean number of colonies per genus per unit area (colonies genus⁻¹ m⁻²) per site or region; and
- (ii) colony surface area values, defined as the mean total surface area of colonies per genus per unit area (m² per m²) per site or region

All taxonomic analyses, ordinations and tests were repeated using both coral genera and coral families (separately) as the unit variable. This entire process was repeated separately for juvenile coral data and adult coral data. Each sample (site) analysed in this way comprised mean average values for each taxon from all replicate transects or quadrats surveyed at that site. The sequence of steps followed in this data treatment and analysis routine is summarised in the schematic diagram Figure 3, illustrating the different stages, variables, transformations and data units used.

5.3.2 Testing the impact of variable replicates within samples (reef sites)

Increasing sampling effort inevitably leads to higher numbers of taxa recorded across all replicates. Thus it was necessary to ensure that any statistically significant differences observed between samples were not an artefact of different numbers of replicates between sites or regions. Further analyses were therefore carried out to examine whether observed differences between sites and regions might be affected by the differing numbers of replicates. This was carried out using bubble plots to superimpose replicate number as an independent environmental variable over the MDS ordinations obtained from the multivariate analyses of site taxonomic composition. In addition, MDS ordinations and ANOSIM testing were repeated using raw replicate data as well as pooled sample data, to monitor the consistency of within-region groupings between the two.

5.3.3 Size frequency distributions of coral communities (pooled taxa)

For analysis of trends in size distribution of corals across the samples (reef sites and regions), the above analytical procedure was repeated, substituting the taxonomic variables with colony size class bins (following the CCCR methodology), with values pooled across all taxa (Obura and Grimsditch 2008).

As before, analyses were repeated with two sets of values calculated from the raw data (colony density values, and colony surface area values), with varying degrees of transformation, and with different value units (colony surface area and density)(Figure 3). Separate analyses were carried out for juvenile and adult communities and in addition, for survey regions at which both adult and juvenile colony data were collected (Table 2), juvenile and adult colony data were pooled to enable analysis of all cohorts within populations. In this case the two data sets were first standardised (colonies per size category per unit area) to account for the different sampling techniques employed for adult and juvenile colonies (transects and quadrats respectively)(section 4; page 61).

5.3.4 Size frequency distributions of coral communities (individual taxa)

The multivariate routines outlined above focused on identifying trends in either the taxonomic composition or the size frequency distribution of coral communities within samples. A third approach classified each sample based on all size frequency distributions of all populations of taxa within the overall reef community, simultaneously. This was carried out by subdividing all taxonomic variables by each of the CCCR size class bins used above, creating enlarged matrices with a maximum of 9 variables per taxon.

The subsequent analytical routine adopted was the same as that followed for taxonomic composition and size frequency distribution matrices (Figure 3), and was replicated:

- (i) at varying degrees of transformation (separately);
- (ii) for colony density values and colony surface area values (separately);
- (iii) for adult and juvenile genera (separately); and
- (iv) for pooled adult and juvenile genera for regions at which both were surveyed.

5.3.5 Matching and comparison of multivariate patterns

Permutation testing was carried out to examine the relatedness of the different multivariate analysis outcomes described above and in Figure 3 for matching groups of samples. The RELATE routine (Clarke and Warwick 2001) was used to calculate relatedness of different Bray-Curtis similarity matrices, across all combinations of values, variables and transformations being used.

These included differences in data values (colony surface area versus colony density); differences in taxonomic resolution (genus versus family); differences in variables (taxa versus size classes); differences in sampling cohorts (adults versus juveniles, as well as pooled cohorts where possible); and analyses under different levels of transformation ($\sqrt{\quad}$, $\sqrt[3]{\quad}$, log, presence/absence). These tests were also carried out against the independently-derived data collected from the same samples, including overall reef benthic composition, based on data obtained from benthic intercept transects and visual estimates (Table 2; page 66).

The ρ coefficients resulting from all combinations of pairwise RELATE tests represent measures of similarity between the different analysis outcomes, with a value of zero when there is no similarity whatsoever between the two. Similarity matrices of ρ coefficients from all pairs of ordinations were used to create 2nd stage MDS ordinations (2STAGE) (Clarke and Warwick 2001) to provide a 2-dimensional representation of the relationship between the multivariate sample patterns under these various data treatments, transformations and analysis approaches.

The objective of this process was to quantify agreement between different multivariate analyses, and to identify how the multivariate patterns changed as a result of the use of different transformations, taxonomic aggregations, and data units, in order to understand how the data treatments influenced the resulting conclusions about between-sample relationships.

5.3.6 Comparison of coral community data against benthic composition data

The above analyses were carried out on data collected from measuring hard corals based on the methods described in section 4.1 and section 4.2; page 61. Additional analyses were carried out data obtained from surveys of the broader reef benthic community (section 4.7.1; page 66).

Non-metric ordinations were repeated from samples based on benthic composition data collected from the Granitic Seychelles and Farasan Banks. Separate analyses were carried out using different variables from these benthic composition surveys. These included:

- (i) coral genera, based on LIT measurements, with units as percentage cover of individual taxa (Granitic Seychelles only);
- (ii) hard coral growth forms (massive, tabular, branching, encrusting, corymbose), based on visual estimates, with units as percentage cover of transect, based on Jennings (1996) (Granitic Seychelles only); and
- (iii) all major substratum and benthic groups (separate live and dead categories of all coral growth forms above, plus sand, rubble, rock, soft coral and macroalgae), based on visual estimates, with units as percentage cover of transect (Granitic Seychelles and Farasan Banks)

In each case, values for each sample used in analyses were calculated as the mean for each site from all replicates. Bubble plots were used as a means of superimposing absolute hard coral cover values on the resulting MDS ordinations. Resulting multivariate patterns were compared with those obtained from analysis of coral community composition data for the same samples, to identify the extent to which the resulting patterns of between sample dissimilarity resembled one another.

This was carried out using the same routine as that outlined in section 5.3.5 above, using the RELATE test to measure the Spearman rank correlation ρ of pairs of resemblance matrices.

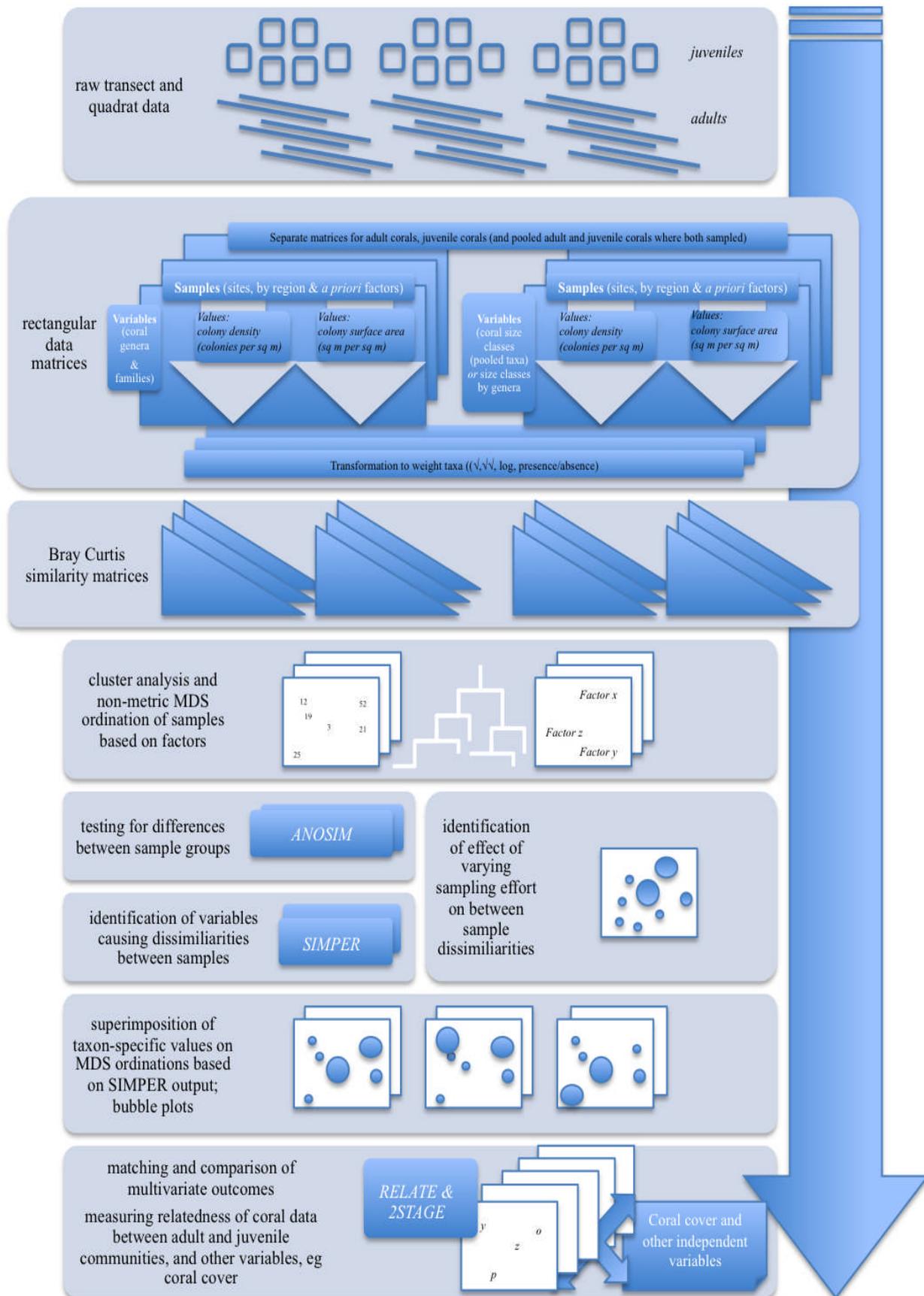


Figure 3. Schematic diagram showing sequence of analytical routines followed during multivariate ordinations and testing

5.4 Taxonomic diversity

Univariate diversity indices were used to reduce multi-taxa assemblage data into a single index for each sample (reef site), based on genus and family-level diversity.

Taxonomic richness was measured by the total number of taxa (genera and families separately) and by the Shannon diversity index (H'). Equitability was measured using Pielou's evenness index (J'). Dominance was measured using the Simpson index (λ). All diversity indices were calculated per site and region, separately for genera and families. Graphical representation techniques were used to plot patterns of relative abundance and dominance of genera between and within regions as follows:

- (i) Genus accumulation curves (Clarke and Warwick 2001) were plotted to show the increasing total number of taxa sampled per region, as successive within-region samples were added in random order. From these curves, the true total number of genera per region that would be observed as the sample effort tended to infinity was estimated.
- (ii) Geometric abundance curves (Clarke and Warwick 2001) were used to give an indication of taxonomic rarity across the 4 survey regions, plotting the number of genera represented by x2 increasing numbers of colonies.
- (iii) Cumulative ranked genus abundance (dominance) plots (k -dominance curves (Clarke and Warwick 2001) were used to rank genera in decreasing order of abundance, plotting each taxon's relative abundance (as a cumulative percentage of the total abundance in the sample) against log taxon rank. Differences between k -dominance curves, across multiple sample groups, were tested using the DOMDIS routine to calculate the 'distance apart' of every pair of cumulative curves (Clarke 1990), and testing for significant differences between groups using ANOSIM.
- (iv) Separate k -dominance curves were plotted from genus abundance and surface area data on the same axes to enable comparison of the forms of the resulting curves. The resulting abundance/area comparison (AAC) plots resemble

abundance/biomass comparison (ABC) plots (Warwick 1986) substituting biomass data with colony surface area values for each genus. The W index (Clarke and Warwick 2001) was used to represent differences between area and abundance curves on AAC plots, providing a univariate index to compare AAC curves between samples and sample groups, as well as a means of testing for significance differences between groups using ANOVA.

These distributional approaches and generic accumulation curves (geometric abundance curves, k -dominance plots and AAC plots) together enabled greater resolution of analysis of taxonomic diversity than was possible from the single summary univariate indices.

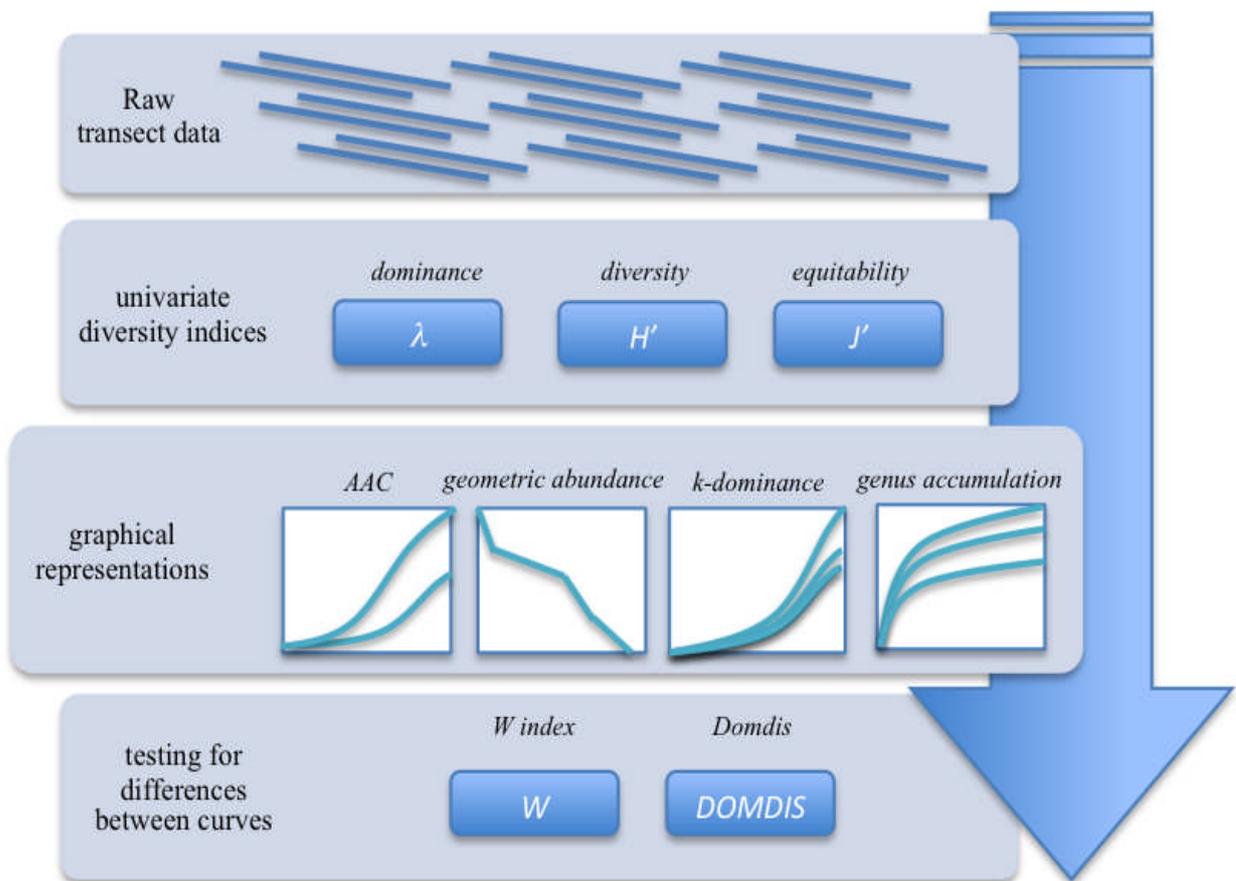


Figure 4. Schematic diagram showing analyses carried out during testing of differences in taxonomic richness between samples

5.5 Testing and comparison of methodological approaches

5.5.1 Ultra-violet juvenile coral assessment

Size frequency distributions of juvenile coral communities recorded with and without the use of UV were compared graphically using both numerical abundance and surface area data. Differences in resulting distributions were tested using two-sample T-tests based on transformed data using the Box-Cox transformation routine described in section 5.2 above.

5.5.2 Effect of genus reduction (CCCR target taxa approach)

The effect of reducing sampled coral taxa to the predefined CCCR list of 21 target genera was examined by removing non-target taxa from data collected in this study. The resulting coral community data were then compared with the original all-genera community to test the validity of the CCCR-derived data.

Size frequency distributions (CCCR taxa only) were compared with those derived from the full complement of genera using two-sample T-tests based on Box-Cox transformed data. Multivariate analyses of size frequency distributions and taxonomic composition (section 5.3 above) were repeated based on the reduced number of taxa, and relationships between the resulting ordinations of between-sample dissimilarity were compared by calculating the Spearman rank correlation ρ of each underlying resemblance matrix, using the RELATE routine (section 5.3.5; page 73).

The BVSTEP procedure (Clarke and Warwick 2001) was also applied to the full genus matrices to produce a smaller subset of genera, whose similarity matrix across all samples correlated closely with that of the full genus set at $\rho \geq 0.95$. This subset of genera was then compared to the CCCR 'target genera' to assess whether these genera are the most influential taxa in terms of differentiating ecologically significant differences between samples.

Finally, analysis of taxonomic diversity indices, generic accumulation and k -dominance curves was repeated using the reduced community of target taxa to assess the impact of sampling a reduced number of genera on the ability of the resulting data to discriminate sites based on environmental disturbance.

5.5.3 Identifying dominant genera driving between-sample differences

Further analyses were carried out in order to establish whether differentiation of samples based on factors identified a priori could be obtained using a statistically identified subset of the total number of genera, and whether this subset matched that selected by the CCCR approach.

In order to do this, the least abundant taxa were first taken out of the analysis altogether, by removing all genera that accounted for less than 5% of the total number of colonies for at least one replicate sample. In other words, a genus was defined as 'important' if it accounted for more than 5% of the total observed number of coral colonies within at least one sample.

Model matrices were constructed based on the factor under investigation. For example, using a factor indicating the presence or absence of mass mortality, a triangular model matrix was constructed recording 0s between samples in the same group, but 1s between all samples in different groups. Models were used to try to match subsets of genera which best differentiated the factor levels (for example high similarity within a group, low similarity between groups).

BVSTEP analysis was then carried out on transformed data from the sample-by-genus matrix (all samples, reduced genera) to produce a subset of genera whose similarity matrix correlated most closely with that of the model matrix (Clarke and Warwick 2001).

RESULTS

6 Overview of benthic composition and reef status of the five regions

6.1 Chagos (2006)

All Chagos atolls showed strong, vigorous recovery after the 1998 mortality event. However the extent of this recovery, and the composition of reef benthic communities around the archipelago, varied greatly between sites.

With very few exceptions (most notably Egmont atoll), at all sites and depths living substrate far exceeded non-living substrate, and hard coral was the most dominant form of living benthos. Peros Banos, Salomon and Great Chagos Bank atolls had greater cover than Egmont or Diego Garcia atolls, with higher levels of hard coral cover, as well as greater prevalence of larger corals. In many sites, coral cover had recovered almost completely, averages ranging from as low as 6% at Egmont to 87% at Diego Garcia. Soft coral cover ranged from being entirely absent at several sites to 30% cover at Peros Banos.

Egmont sites were affected by a severe mortality event in the 12 months prior to surveying, which killed over 95% of hard coral on shallow reefs as well as dramatically reducing juvenile colony abundance (Harris and Sheppard 2008). The substrate here was covered almost entirely by large dead *Acropora cytherea* and some *A. clathrata* table corals up to 3.75 m in diameter. The collapse and erosion of these tables also caused further mortality by scouring of other corals on the outer reef slope down to 15 m depth.

Other between-atoll differences were equally clear. Diego Garcia's reef communities showed higher levels of soft corals and sponges, and generally lower coral cover. Eastern Salomon atoll had recovered much less than the west; the former site was previously dominated by soft corals, which appear in all sites to have recovered much

less successfully to date than have the stony corals. By 2010 however, soft coral had returned to pre-1998 levels (Sheppard pers. comm.).

Broad differences between lagoonal patch and outer reef slope communities were observed during the study, with lagoonal reefs generally showing far higher coral cover than outer slopes, composed of larger, older colonies, in particular branching and tabular *Acropora* spp. (one-way ANOSIM from benthic PIT data, global $R = 0.72$, $p < 0.1$).

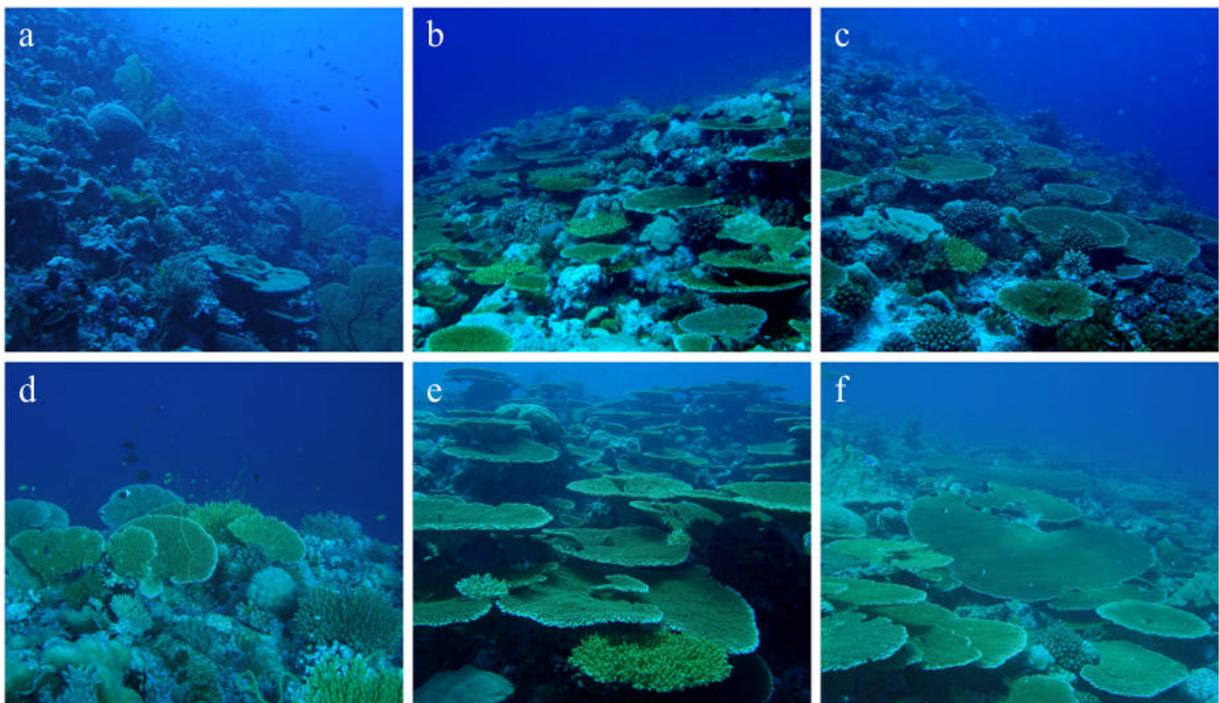


Figure 5. *Acropora*-dominated outer reef slopes in the Chagos archipelago (March 2006), showing clear recovery of reefs following documented bleaching-related mass mortality in 1998 and subsequently

6.2 Granitic Seychelles (2008)

Coral communities were generally situated on flat sandy or calcareous substrata at the survey depth, or on steeply shelving granite boulders reaching the seabed at 10-12m. Most reefs on sandy or carbonate substrata were extremely depauperate, with low coral cover (Figure 6), heavily eroded reef frameworks, and highly variable abundance of erect macroalgae; ranging from absence of seaweeds at 9 of 22 sites, to 70% ($\pm 3\%$ SE) -predominantly *Sargassum* and *Lobophora* spp. - at Praslin Southwest Carbonate.

Reefs on sandy or carbonate substrata showed signs of recent collapse of the framework, with a high degree of bioerosion (Figure 9 and Figure 10). Although some live colonies remained, including large old *Porites* and *Acropora* colonies, mature corals were generally isolated surrounded by large tracts of mobile coral rubble, macroalgae and sand. At a number of carbonate sites the seabed was covered in a film of cyanobacteria, with anoxic conditions within the sediment (Figure 10). Coral rubble was generally loose and juvenile corals were in notably low abundance. An exception was the carbonate reefs around Cousin Island, adjacent to Praslin island, where the exposed conditions had removed loose rubble leaving a hardened largely uncolonised coral rock framework across large areas.

Several carbonate and patch reef sites (as classified by Jennings 1996) showed patches of corymbose *Acropora* species, with areas of thriving regrowth covering continuous broad expanses of seabed (Figure 7). While these patches did not dominate any of the sites visited, they illustrate the considerable spatial heterogeneity within some sites. Indeed, large expanses of these reef sites, particularly those around the island of Praslin, showed negligible coral cover. Many replicate transects recorded no adult or juvenile colonies, even when surveying was supported by ultraviolet census to aid detection of cryptic colonies. Juvenile and adult coral abundance at these sites were the lowest of any reef regions studied (see also Figure 43; page 129).

Reefs on hard granitic substrata (the 'granite' geomorphological class of samples from Jennings 1996) generally supported much higher abundance, cover and complexity of corals. They exhibited very high densities of small encrusting flat faviid colonies growing directly on granite boulders, particularly *Favia* spp., *Favites pentagona* and *Goniastrea* often leaving little uncolonised substratum. Several of these sites also showed prolific growth of branching and tabular *Acropora* species, notably *A. clathrata*, *A. abrotanoides*, and *A. pulchra*.

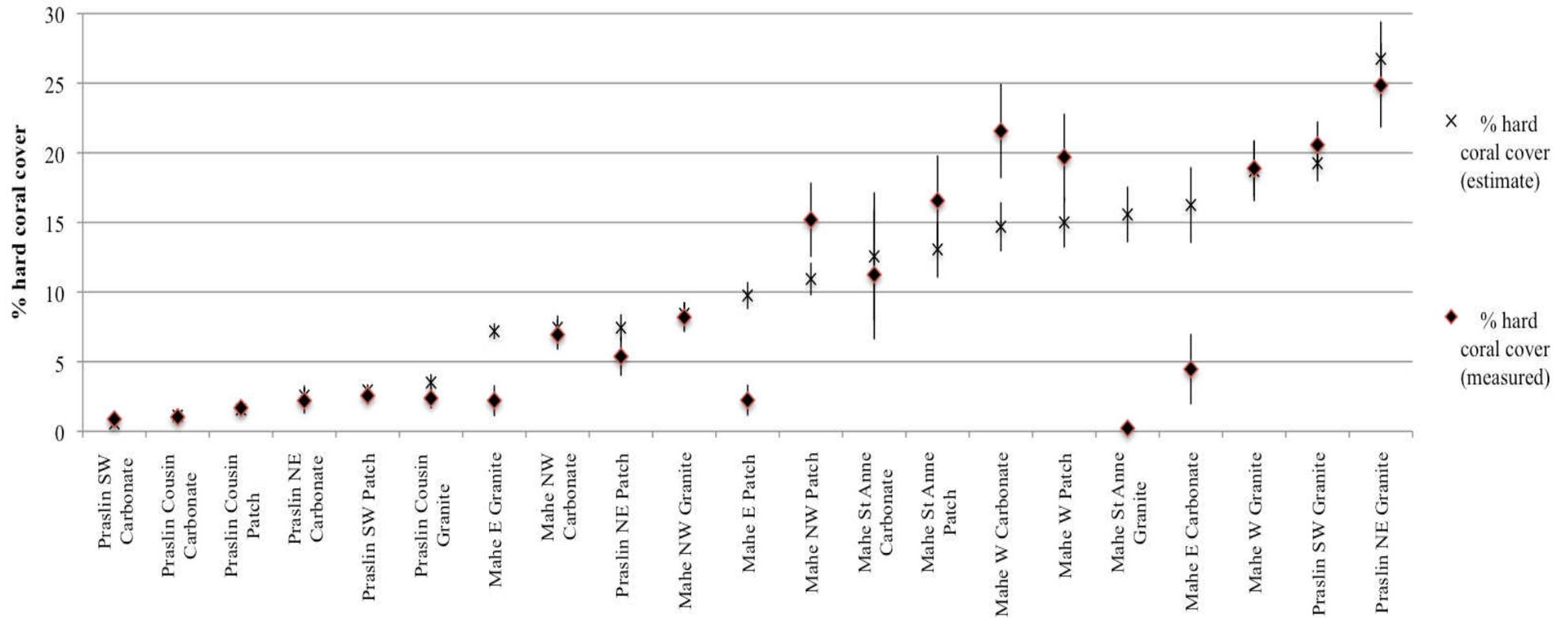


Figure 6. Mean % benthic cover of hard coral (\pm standard error) based on benthic intercept measurements and visual estimates, across all sites in the Granitic Seychelles, ranked in order of increasing estimated coral cover

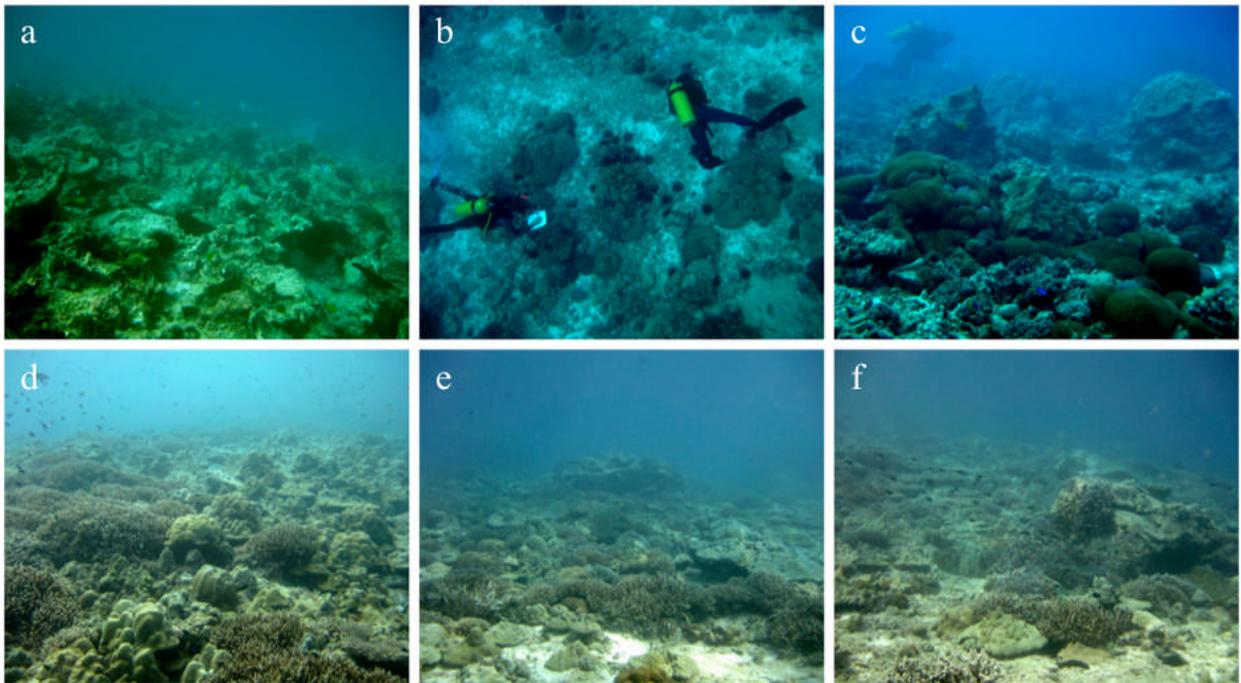


Figure 7. Reef sites from the Granitic Seychelles: (a) hardened dead coral framework at Cousin island marine reserve. Some areas of the island's carbonate reefs were unusual in that, despite being largely devoid of living corals, the underlying dead reef substratum had not yet collapsed; (b) and (c) illustrate the low abundance of corals at carbonate reef sites, with large remnant *Porites* and *Goniopora* colonies; (d), (e) and (f) show recovering carbonate reef sites, dominated by fast growing *Acropora*

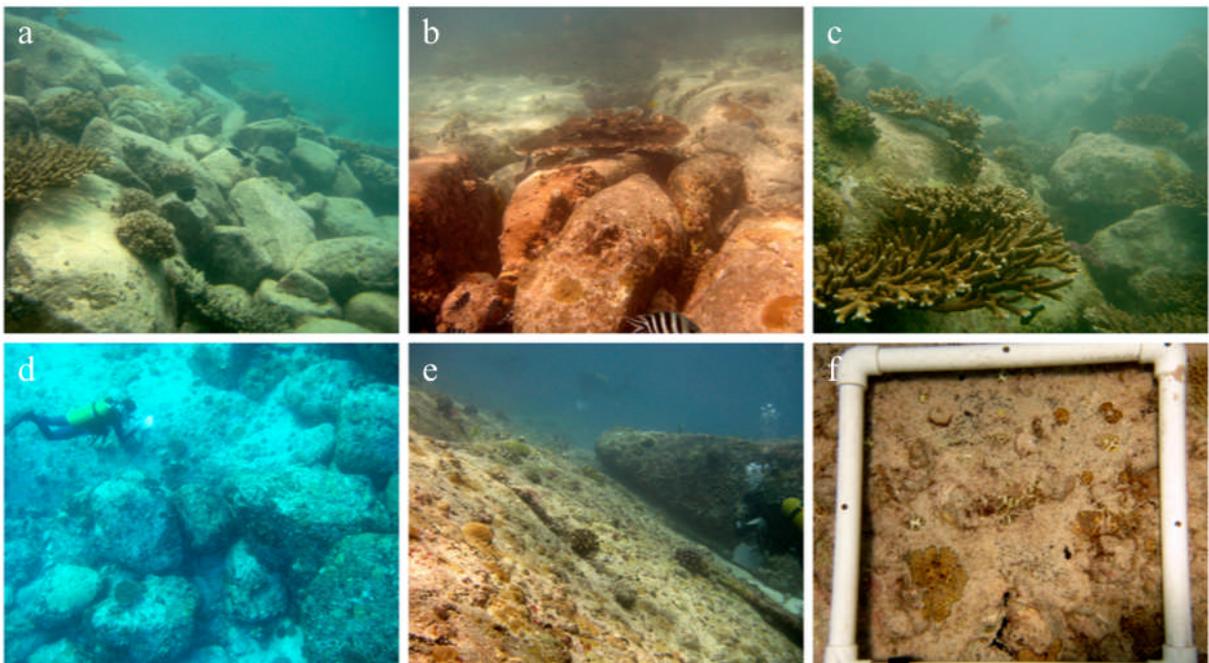


Figure 8. Granite reef sites within the Granitic Seychelles. These sites show low macro-algal cover, and are characterised by branching acroporids growing directly on the hard substratum, as shown in images (a), (b) and (c). (d), (e) and (f) show the high abundance of juvenile encrusting faviid colonies found at these sites

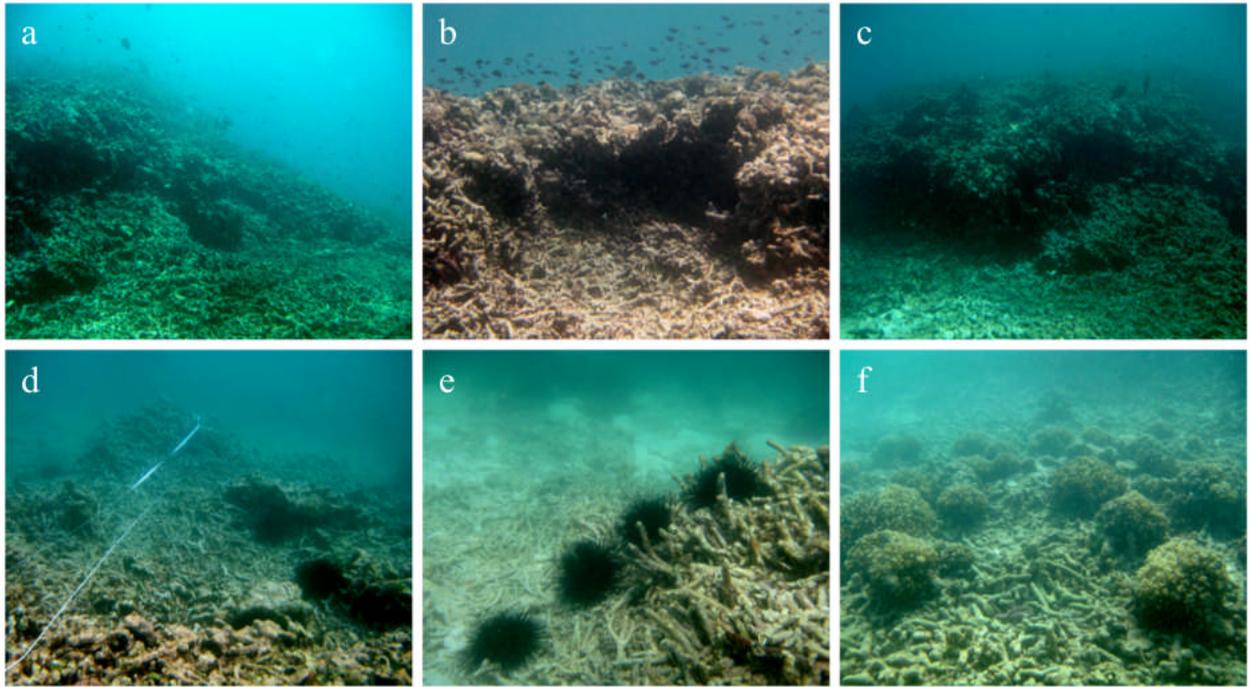


Figure 9. Reef framework collapse in the Granitic Seychelles following bioerosion of dead colonies in marine reserves at Cousin Island, Praslin; (a), (b) and (c), and St Anne Island, Mahe; (d), (e) and (f). Image (f) shows recolonisation of dead coral rubble by fast growing *Pocillopora* colonies

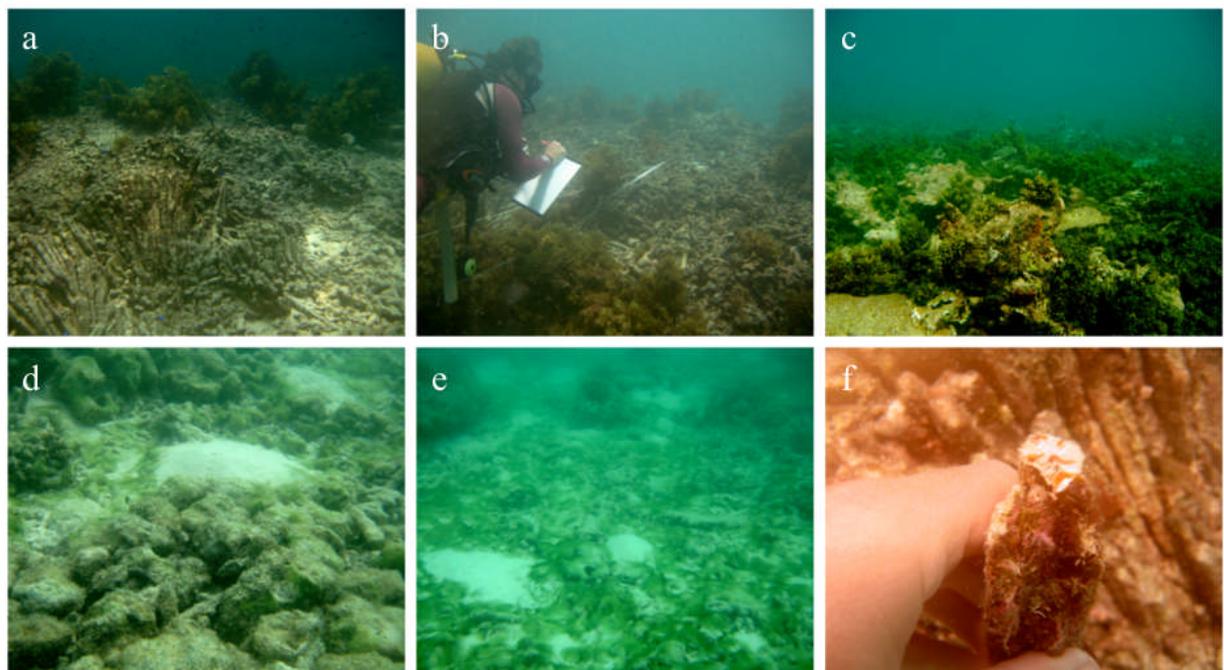


Figure 10. Overgrowth of collapsed reef framework by macro-algae and cyanobacteria at in marine reserves in the Granitic Seychelles. (a), (b) and (c); *Sargassum* dominance on dead reef frameworks in Cousin Island, Praslin. (d) and (e); cyanobacterial film covering substratum in St Anne marine park, Mahe. (f); bioerosion of coral rubble in Cousin Island.

6.3 Farasan Banks, Saudi Arabia (2009)

The benthic environment of most sites surveyed was dominated by hard corals, either living (mean 28.9% cover \pm 2.5 SE; ranging across sites from 7.5% \pm 2.5 SE to 55.0% \pm 5.0% SE) or standing dead colonies (mean 10.0% cover \pm 2.0 SE; ranging across sites from total absence to 43.0% \pm 2.5% SE), with moderate soft coral cover at most sites (mean 19.0% cover \pm 3.8 SE), and negligible macro-algal cover at almost all sites (ranging from total absence at 34 of 52 sites, to 30% at one site; mean across all sites 4.5% cover \pm 0.8 SE).

Reefs surveyed were characterised by steep vertical or overhanging walls dominated by *Porites* spp., descending to >60m from a reef crest at 3-5 m (Figure 12). A shallow reef flat above the reef crest had variable coral cover depending on its degree of exposure. The shallow-water zones above the reef crest was generally overwhelmingly dominated by a *Porites* framework, although some sites showed abundance of other taxa in this higher-energy environment, notably survey sites 18, 27, 28 and 51, which exhibited almost complete coverage of diverse *Acropora* spp..

An overhanging indentation in the reef wall, creating a cave recessed approximately 2-5 m into the reef platform, was a common feature of many sites at approximately 15 m depth (Figure 12). The inshore reef sites generally had a shallower gradient, with the reef slope terminating on sandy seafloor at between 15 - 35 m depth. High turbidity prevailed at all inshore reef sites surveyed, with corals more commonly growing in plating growth forms beneath 10 - 15 m, particularly *Echinopora*, *Mycedium*, *Acropora* and *Montipora* spp..

Almost all sites showed very high structural complexity, with reef architecture invariably dominated by massive *Porites* colonies (Figure 12 and Figure 13). Coral cover was lowest on reefs with the highest relief, which in many cases was vertical to depths \geq 60 m. Where coral cover was low, space was generally occupied by sand or bare coral rock, with little evidence of macroalgal competition for space on the substratum. A pronounced zone of foliose *Echinopora* spp. zone was common in many outer reef slopes, at a variable depth of 15 – 25 m.

Notwithstanding the high structural complexity of the reefs surveyed, 20 of the 54 sites visited showed distinct evidence of recent widespread coral mortality, with several sites having shown almost complete mortality of all adult corals. Most notably, at survey sites 8, 17, 41, 45 and 42 (Figure 14), almost all adult colonies were dead at the survey depth, with mortality in some cases extending from the surface to a depth of at least 55 m. Across all sites, live hard coral was negatively correlated to dead coral (Pearson $r = -0.35$, $p = 0.017$)(Figure 11).

At all such sites, the dead colony structures and reef framework remained intact, with dead skeletons generally identifiable to genus or species, and little or no turf or macro-algal coverage. The underwater aspect of these dead adult coral communities was striking, constituting an architecturally extremely complex yet entirely colourless grey reef framework. Newly recruited juvenile corals were present in extremely high abundance at all these sites.

The cause of the mortality was not clear, although predation of colonies by *Acanthaster planci* was observed at many sites. Over 500 feeding starfish were recorded within ~100 m along the outer reef slope of one survey dive alone. The approximate date of mortality of affected sites could not be inferred from the dead colonies, but was estimated to have occurred not more than 1-2 years earlier, based on the low degree of erosion of the remaining standing coral framework, discolouration of the dead colonies, the presence of algal turfs, and the recorded size structure newly colonising juveniles.

Further indications that mortality was caused by *Acanthaster planci* rather than warming came from the observation that where mortality was most pronounced on the reef slope at the survey depth of 10m live adult colonies were abundant in very shallow water above the reef crest.

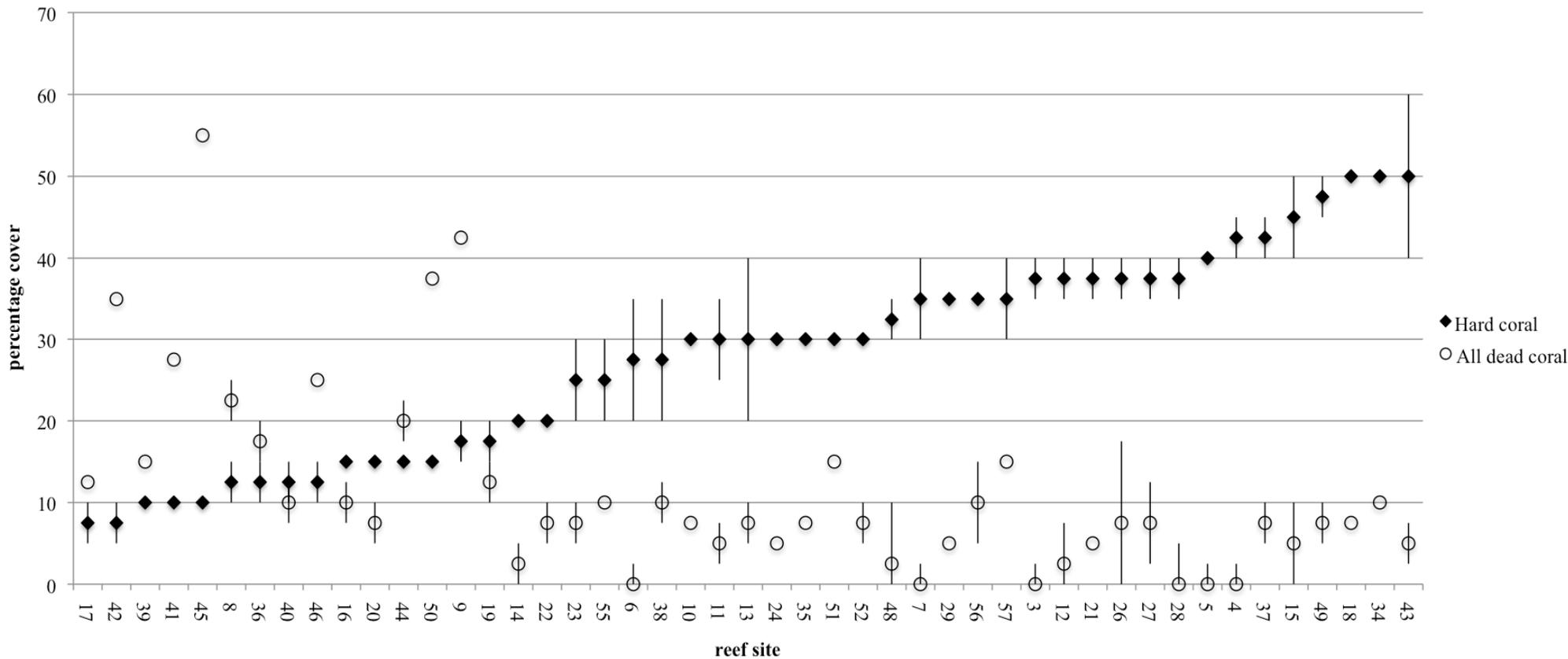


Figure 11. Mean % benthic cover of live hard coral and dead standing coral (\pm standard error) across all sites in the Farasan Banks based on visual estimates (Pearson $r = -0.35$, $p = 0.017$). Sites ranked by increasing cover of hard coral

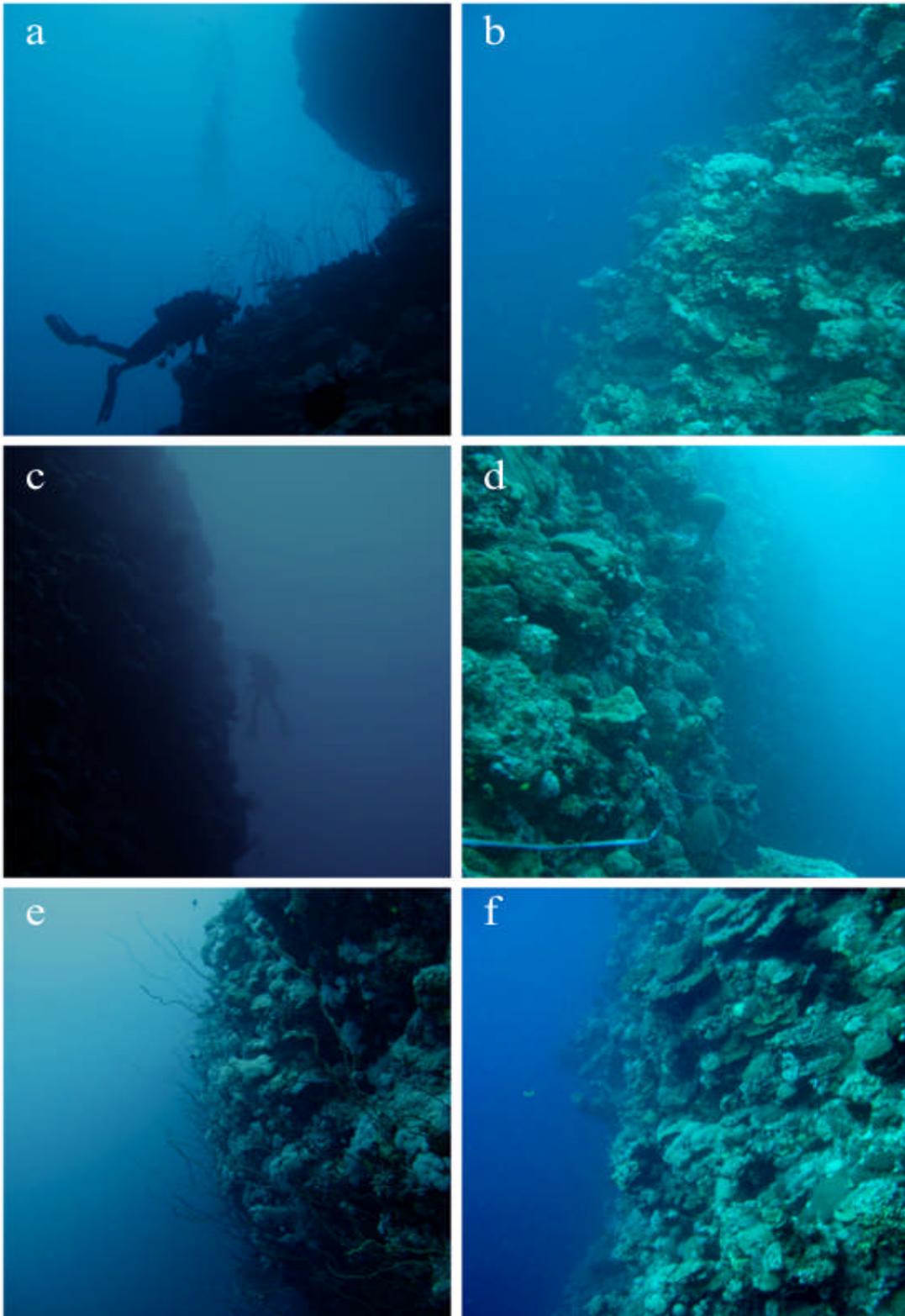


Figure 12. *Porites*-dominated reef slopes in the Farasan Banks, Saudi Arabia (April 2009). The very steep gradient of these reefs is characteristic of the reef sites surveyed. Image (a) shows the overhanging indentation in the reef slope typical of many sites at 12-15m depth.

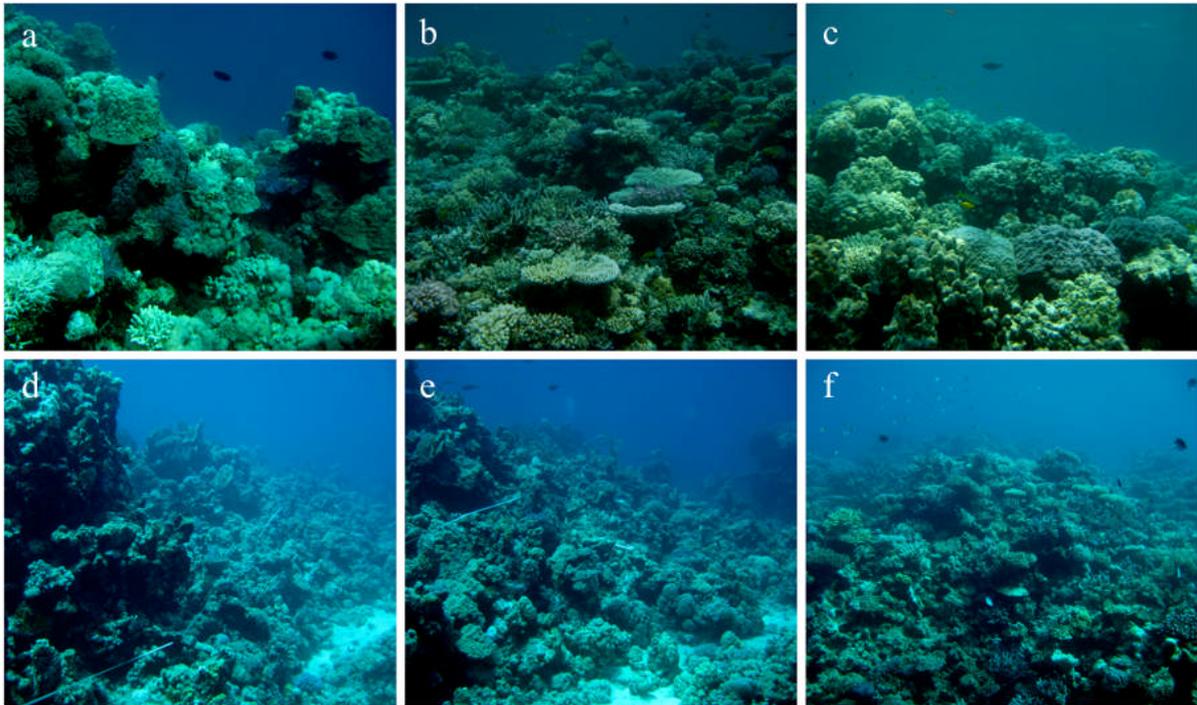


Figure 13. Shallow coral reefs (7-10m depth) of the Farasan Banks, Saudi Arabia (April 2009), illustrating the very high structural complexity of these *Porites* spp.-dominated habitats. The very high architectural rugosity of these habitats demonstrates how total colony surface area can greatly exceed a 2-dimensional planar transect area. Image (b) shows an atypical reef crest dominated by *Acropora* spp.

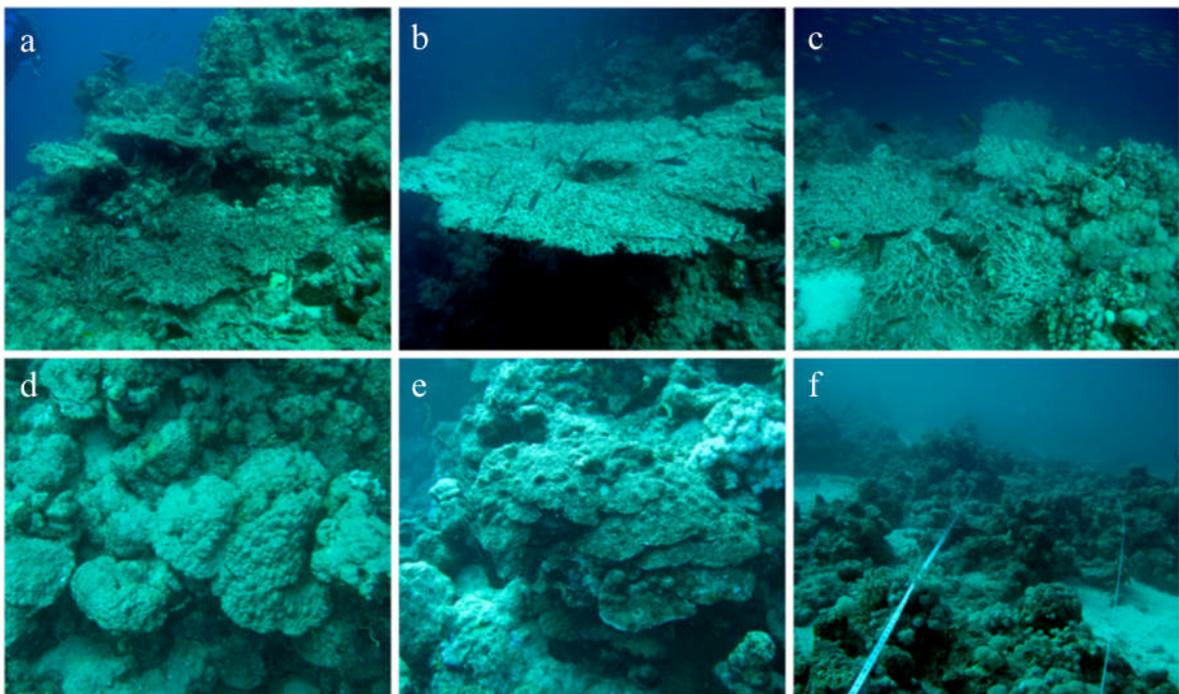


Figure 14. Mass mortality of hard corals in the Farasan Banks, Saudi Arabia at 10 m depth (April 2009). The benthos consists almost entirely of dead, largely uncolonised hard coral, with mortality affecting taxa present. These sites were classified as showing 'severe' mortality because of the near total absence of living corals

6.4 Andavadoaka, Madagascar (2008)

Most near shore and offshore fringing reefs were heavily degraded across this study region, with almost all sites dominated by macroalgae communities. Seaward reefs generally had <25% coral cover, with high or dominant levels (35-80% cover) of turf and macro-algae, particularly *Lobophora* sp., *Dictyota* sp., and *Turbinaria* sp. This is a markedly degraded condition from that earlier described by Pichon (1978).

Faviidae, Poritiidae, Agariciidae, and Mussidae were commonly dominant corals at all depths and in all three geomorphological classes of reef (Nadon *et al.* 2007), although much of the eroded coral framework in these areas suggests that most sites were previously dominated by branching *Acropora* spp..

On exposed seaward sites the collapsed reef structure had generally been smoothed into planar surfaces by wave action and appeared to be stabilised by encrusting turf and calcareous algae. Conversely, the substrate of many sheltered fringing reefs and lagoonal patches was loose and unconsolidated coral rubble. Such a highly mobile substratum may limit reef recovery in the region by preventing effective hard coral recruitment.

Reef health was not consistently poor. Considerable heterogeneity of reef condition was observed both between and within survey sites. Offshore patch reef communities protected within the Velondriake locally managed marine area (LMMA) were largely coral-dominated, with prolific coral cover >60% recorded at all depths (7 – 25 m)(Figure 15).

These patch reefs also support diverse coral communities that consist largely of *Acropora* and *Montipora* spp. that either survived earlier bleaching events or had since recruited. Over 130 species of coral have been identified on these patch reefs; a more thorough inventory is likely to yield considerably more, especially as species of *Montipora* and *Acropora*, important framework building genera within the patch reef remain poorly sampled.

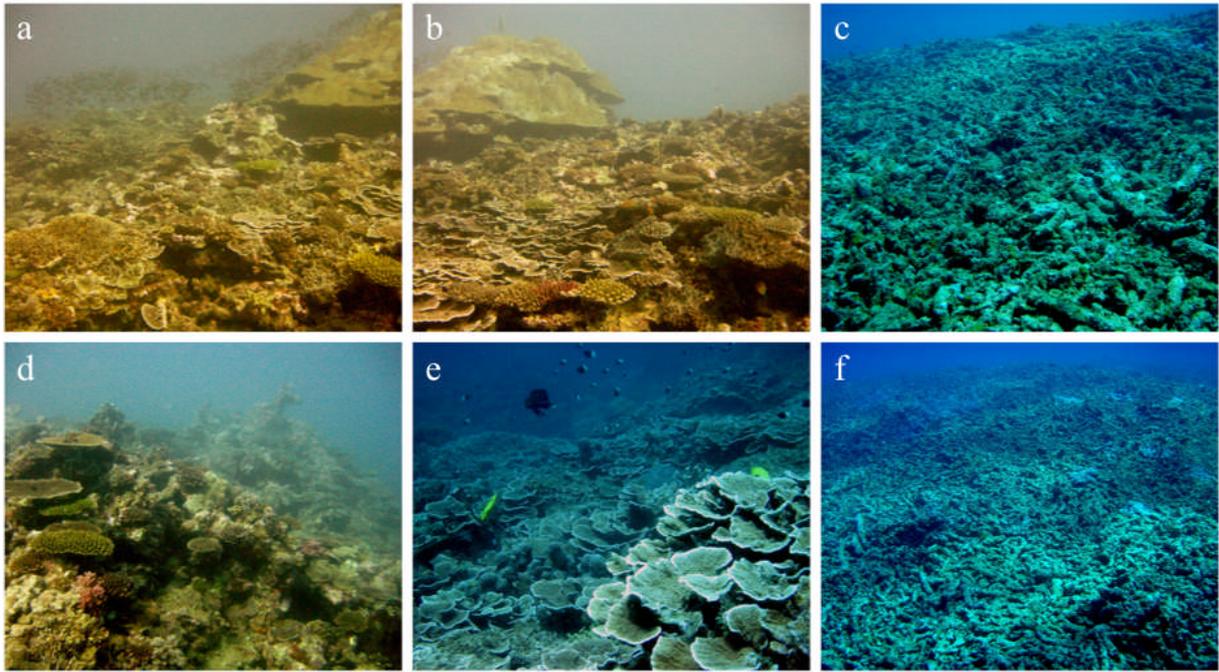


Figure 15. Differential recovery of lagoonal patch reefs in Andavadoaka, southwest Madagascar (June 2008). Images (a), (b), (d) and (e) show highly structurally complex coral-dominated reefs within the Velondriake LMMA, having recovered from a very degraded state since 2003. The acroporid *Montipora aequituberculatica* (e) is a common dominant species at these sites. Images (c) and (f) are characteristic of adjacent lagoonal patch reefs of similar size to those shown in (a), (b), (d) and (e), but which have shown no recovery, possibly on account of their present-day benthic composition consisting almost entirely of unconsolidated mobile coral rubble (collapsed and heavily eroded *Galaxea fascicularis*)

6.5 Toliara, Madagascar (2008)

Reef communities on the outer barrier reef of the city of Toliara were in similar condition to the barrier reef sites ~200 km further north in the Andavadoaka survey region. At the sites measured with LITs, hard coral cover averaged $13\% \pm 5.0$ SE, with the coral community dominated by small predominantly encrusting and massive colonies within the Poritidae and Faviidae, <1 m maximum diameter.

Only $1.6\% \pm 1.3$ SE of the benthic composition comprised structurally complex hard coral growth forms (branching, digitate or tabular colonies). Architectural complexity was thus very low, with little coral framework development above the hard coral rock substratum. Macroalgal cover was consistently higher than hard coral cover (Figure 16). The large stands of *Acropora* of all kinds previously recorded by Pichon (1978) were missing, with no remaining evidence of any dead or eroded tabular coral framework. Water clarity was very high on the outer reef slope, despite extremely high turbidity within the adjacent lagoon, attributed to terrigenous runoff and pollution.

More turbid conditions have been observed during the austral summer rainy season, when the adjacent Onilahy River creates a large sediment plume. Like the exposed reefs further north, the reef substratum was free of mobile dead coral rubble, presumably on account of the scouring effect of the strong prevailing south-westerly swell. Comparison with the equivalent data from Pichon (1978) demonstrates the poor condition in 2008 (Figure 16)(13% \pm 5.0 SE).

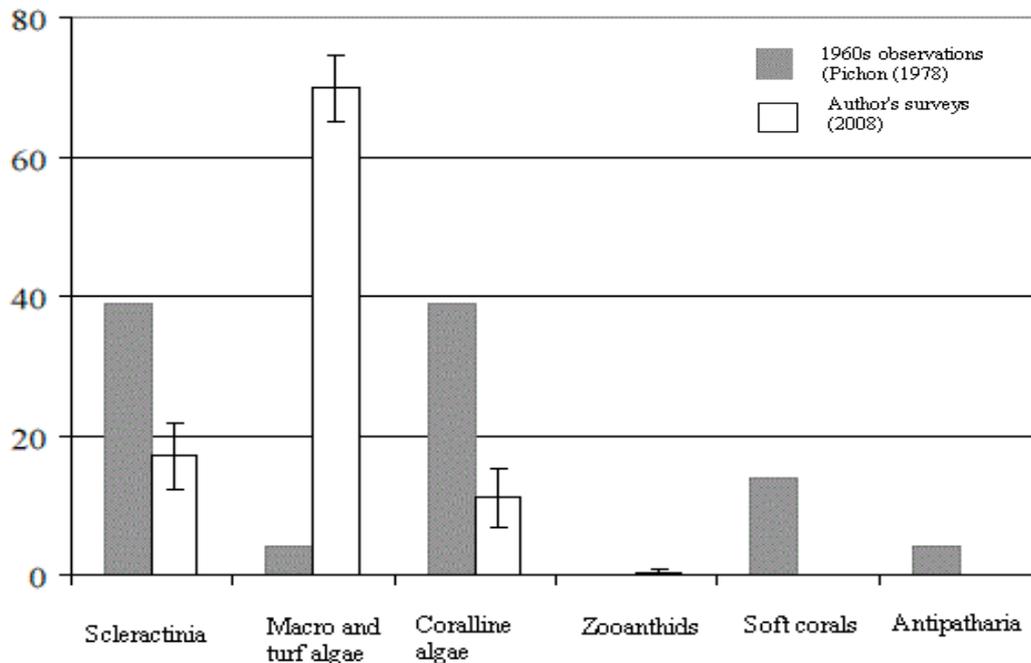


Figure 16. Change in benthic composition of Toliara barrier reef, 1960s - 2008, showing changes in dominant benthic groups. Mean % cover \pm SE (graph from Harris et al. 2010)

7 Coral community analyses

Across these four survey regions this research sampled a total of 403 x 10 m² belt transects and 2977 x 0.11 m² quadrats, identifying and measuring a total of 25,416 hard corals, comprising 18,963 adult colonies (>10 cm) and 6,453 juvenile colonies (\leq 10 cm) from 52 genera and 16 families. The large sample size, capturing data both on taxonomic and size distribution parameters of populations and communities, enabled a number of different analytical approaches to be adopted. These are presented in the order of the data analysis routine discussed in the methods section (section 5; page 67) and summarised in Figure 3.

7.1 Coral communities; summary statistics and graphical representations (pooled taxa)

This section presents summary statistics and graphical representations of data collected from the five non-CCCR reef regions studied in this research, describing density, surface area, and size frequency distributions of juvenile and adult corals for pooled taxa. The relationships between coral surface area and coral cover, and between coral cover and juvenile colony density, are also described. Section 7.1.1 summarises data on density and total surface area of coral communities at each region studied, using aggregated community data for either juveniles or adult colonies. Section 7.2.2 subdivides these values into 9 colony size classes and high-resolution 1 cm size distributions, both within and between regions.

7.1.1 Colony density and total colony surface area (pooled taxa)

Coral colony density and total colony surface area varied enormously between sites both within and between survey regions. Mean colony density and surface area values for each region are shown for adult and juvenile corals in Figure 17 and Figure 18 respectively.

Across all reef sites from all survey regions, the minimum adult colony density was 0.26 colonies m⁻² (\pm 0.12 SE), equivalent to a total coral area of 0.01 m², found at Praslin, Granitic Seychelles (site 'Praslin southwest carbonate'). Maximum adult colony density was over 75 times greater, with 19.5 colonies m⁻² (\pm 3.1 SE), equivalent to a total coral area of 1.08 m², recorded in the Farasan Banks, Saudia Arabia (site number 5).

For juvenile corals, minimum colony density was 0.36 colonies m⁻² (equivalent to a total coral area of 0.0005 m²), again at the same highly depauperate site at Praslin Island in the Granitic Seychelles. Maximum juvenile colony density was 470 times greater, with 169.2 colonies m⁻² recorded (equivalent to a total coral area of 0.22 m²) again in the Farasan Banks (survey site number 45).

Variance of adult colony density within regions was greatest in Madagascar, with within-region standard error in the Toliara and Andavadoaka survey regions being

20% and 17% of the regional mean colony density values respectively. Lowest variance of adult colony density occurred at the Farasan Banks, Saudi Arabia, where between-site standard error was less than half that of the Madagascar sites, at 8% of the between-site mean (Figure 17).

For juveniles, intra-region variance in colony density and total colony surface area was generally relatively lower than adult colonies. The Farasan Banks recorded the lowest variance in colony density (standard error 8% of between-site (intra-region) mean), while the highest variance density was recorded in the Granitic Seychelles (standard error 18% of between-site mean).

These values of colony density, total surface area, and intra-region variance fall broadly within a similar range to results obtained from comparative CCCR studies (Figure 17 and Figure 18). Notable exceptions are Al Wajh, Saudi Arabia, where adult colony densities exceeded those recorded in this study (Figure 17) and Northwest Madagascar, where juvenile colony densities were below those recorded in this study (Figure 18).

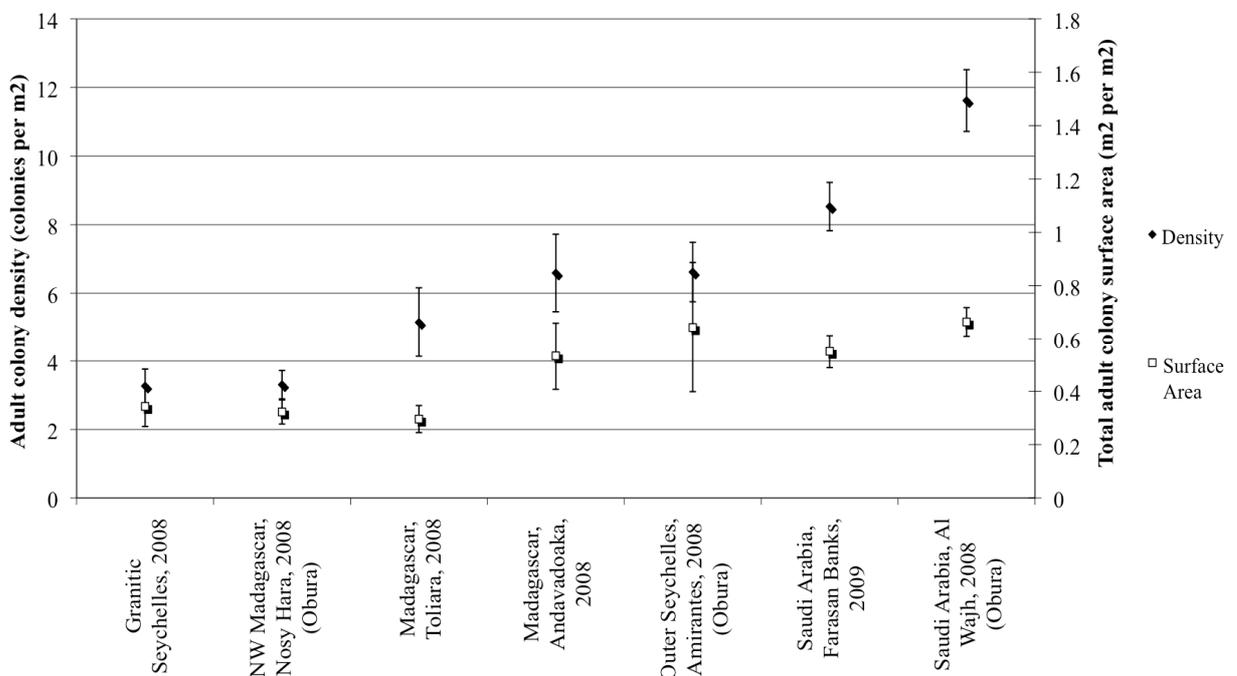


Figure 17. Adult corals: average density and total surface area (\pm standard error), across all regions surveyed in this study, with comparative data from IUCN CCCR studies (regions ordered in sequence of increasing colony density). CCCR sites labeled Obura. Regions ranked by increasing colony density

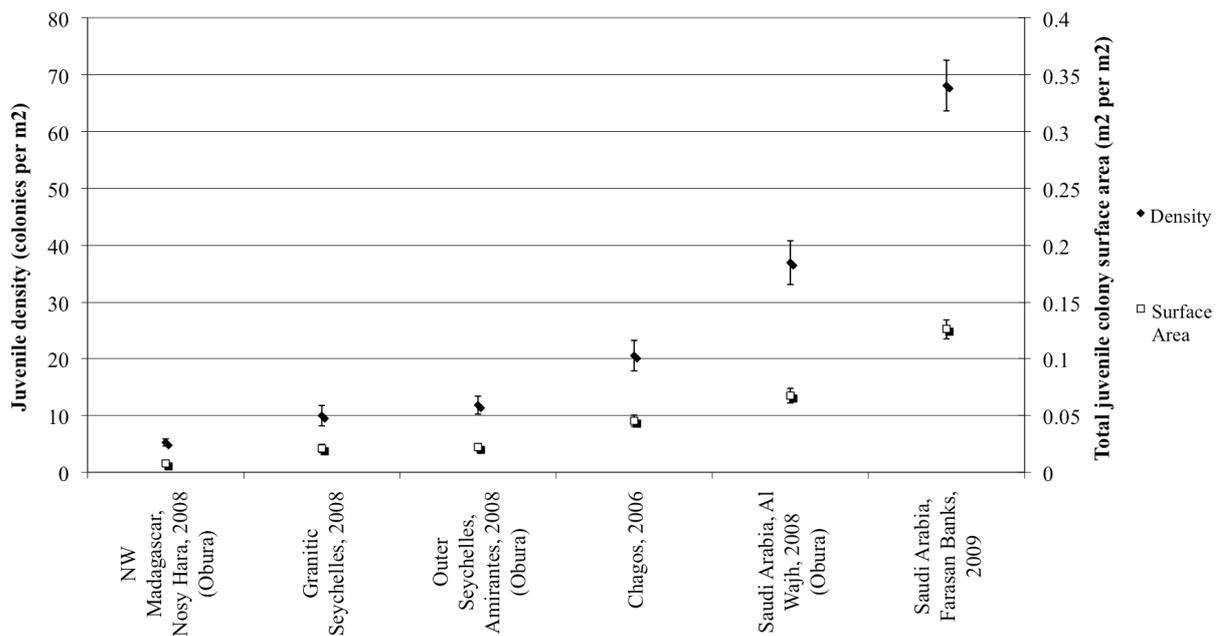


Figure 18. Juvenile corals: average density and total surface area (colonies ≤ 10 cm maximum diameter, \pm standard error), across all regions surveyed in this study, with comparative data from IUCN CCCR studies (regions ordered in sequence of increasing colony density). CCCR sites labeled Obura.

7.1.2 Colony size frequency distribution (pooled taxa)

7.1.2.1 Between-region differences

Higher resolution information is obtained from breaking down the pooled size frequency values into different size classes. The average size frequency distribution of corals at each survey region, based on colony density and surface area, was plotted against comparative data from the CCCR survey regions, with corals binned into the 9 size categories used by the CCCR methodology to enable comparison of all seven different reef regions (Figure 19, Figure 20).

With the exception of Chagos, for which adult coral data are not available, juvenile and adult coral data were standardised within the same plot to enable amalgamation of data from the two sampling approaches (transects and quadrats) within each region, creating a continuous average size frequency distribution for each region across all 9 size categories.

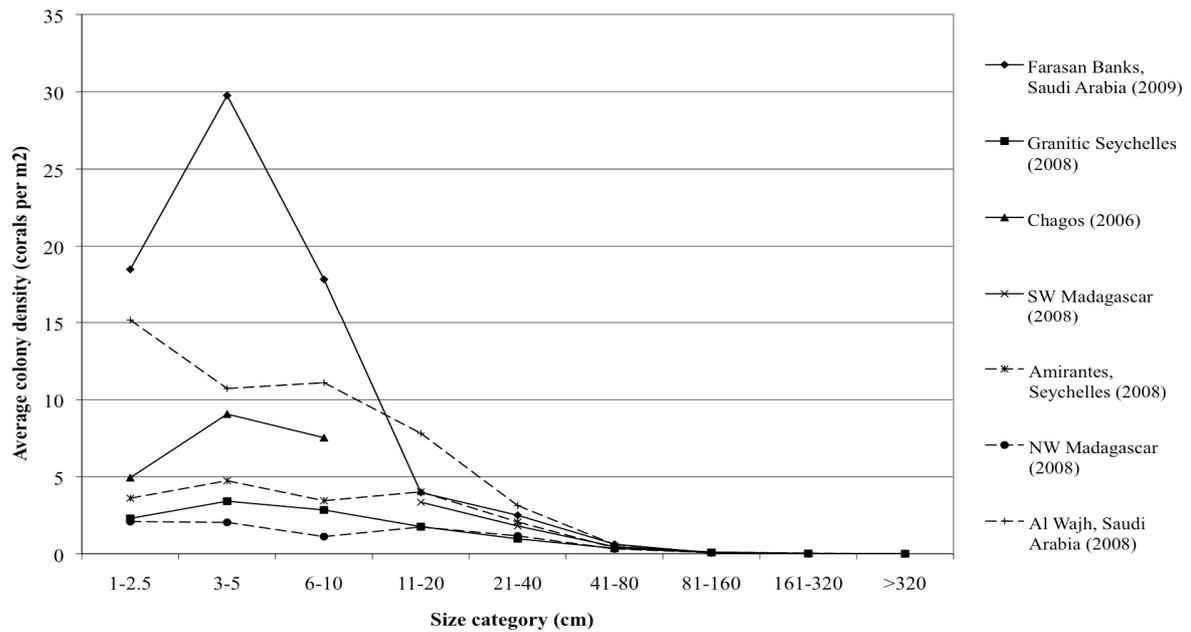


Figure 19. Colony density by size class (all taxa), mean values across all regions with comparative data from IUCN CCCR studies (broken lines)

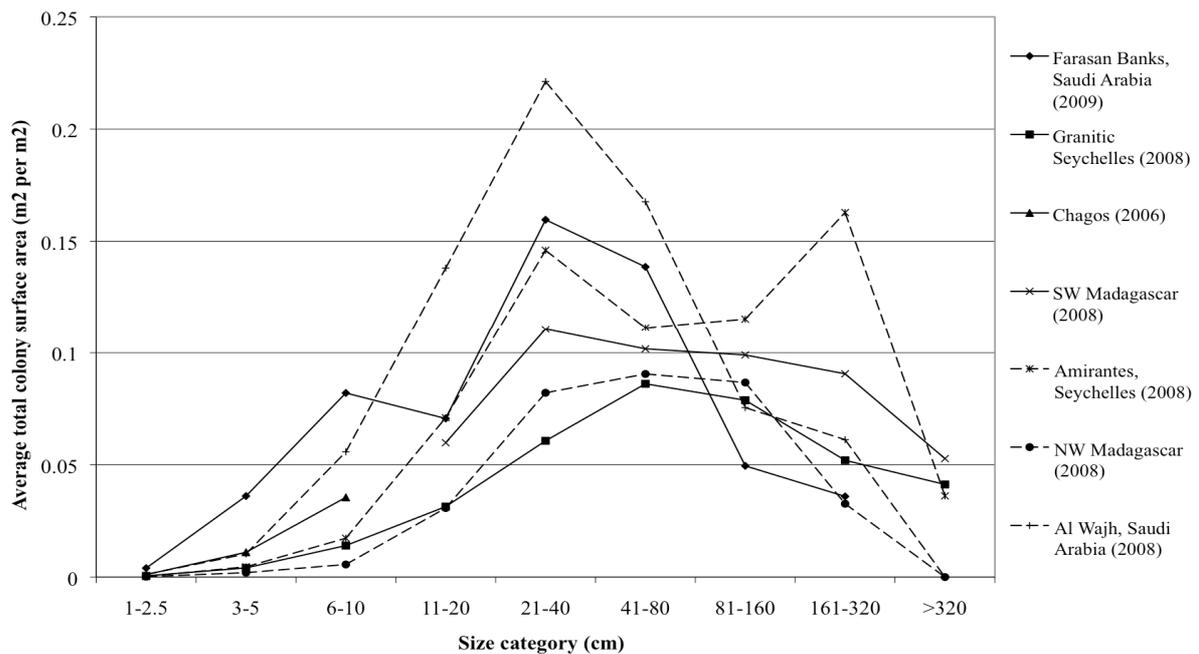


Figure 20. Total hard coral surface area by size class (all taxa), mean values across all regions with comparative data from IUCN CCCR studies (broken lines)

Several important features of the size frequency distributions are evident. All those based on colony density data show distinctly positively (right) skewed frequency distributions, i.e. with a longer right tail, while those based on area data generally show a more normal or left-skewed distribution.

These different shapes are explained by the non-linear relationship between colony diameter and surface area, as is emphasised by the very small contribution to coral surface area made by the extremely high numerical abundance of juvenile colonies in the Farasan Banks. This is also demonstrated by the marked increase in average colony surface area seen in the 161-320 cm size class from the Amirante islands (Outer Seychelles) in Figure 20; this large jump in colony area is not reflected at all in the colony density plot in Figure 19, showing that a small number of very large colonies can have a major impact on total colony surface area thus influencing the upper margin of the surface area curve.

These plots also illustrate the broad similarity in the pattern of size frequency distributions of pooled taxa across the seven regions, despite the considerable differences between regions in overall colony abundance (section 7.1.1).

Notwithstanding these broad patterns, these plots illustrate important differences in the overall size structure of the coral communities between regions. For example, the total colony surface area of Farasan Banks reefs is dominated by corals in size class 21-40 cm, whereas in the much more depauperate Granitic Seychelles, total colony surface area is dominated by considerably larger corals in the two size categories from 41-160 cm (Figure 20). This difference is even more pronounced in Al Wajh, Saudi Arabia, where colonies in size class 161-320 cm dominate the coral community's combined surface area. The significance of these differences is examined in section 7.2; page 106.

The above plots include data from CCCR sites as well as those in this study; the sites of this study alone can be plotted at a finer resolution using the raw data rather than binned categories. Figure 21 and Figure 22 show these data for juvenile and adult colonies respectively for the survey regions visited in this study.

The positive (right) skew for size frequency distributions based on colony abundance data is again apparent within both adults and juveniles. In all regions the frequency of juvenile colonies increased from size category 1 to 3 (0-10mm and 20-30mm maximum diameter respectively), then decreased with increasing colony size (Figure 21).

The shapes of juvenile coral size frequency distributions are broadly similar across regions, however the absolute values of colony density and total surface area of colonies varied considerably. For juvenile colonies, the Farasan Banks are consistently higher in abundance and surface area across all size categories, with coral density of the smallest size categories in some cases up to eight times higher than that recorded in the Granitic Seychelles.

For adults (colonies >10cm maximum diameter), colony size frequency decreased with an approximate power relationship with increasing maximum diameter in all regions. However the left skew for size frequency distributions based on surface area data (Figure 20) is no longer apparent in adult colonies; the higher-resolution raw data reveal more u-shaped distributions at all regions, with the numerically-dominant small adult corals contributing more to total coral surface area than the larger but less abundant mid-size corals (Figure 22). Total colony area increased with maximum diameter following an approximately 2nd order polynomial relationship. Both trends are illustrated using pooled data from all taxa and sites for each region in Figure 22.

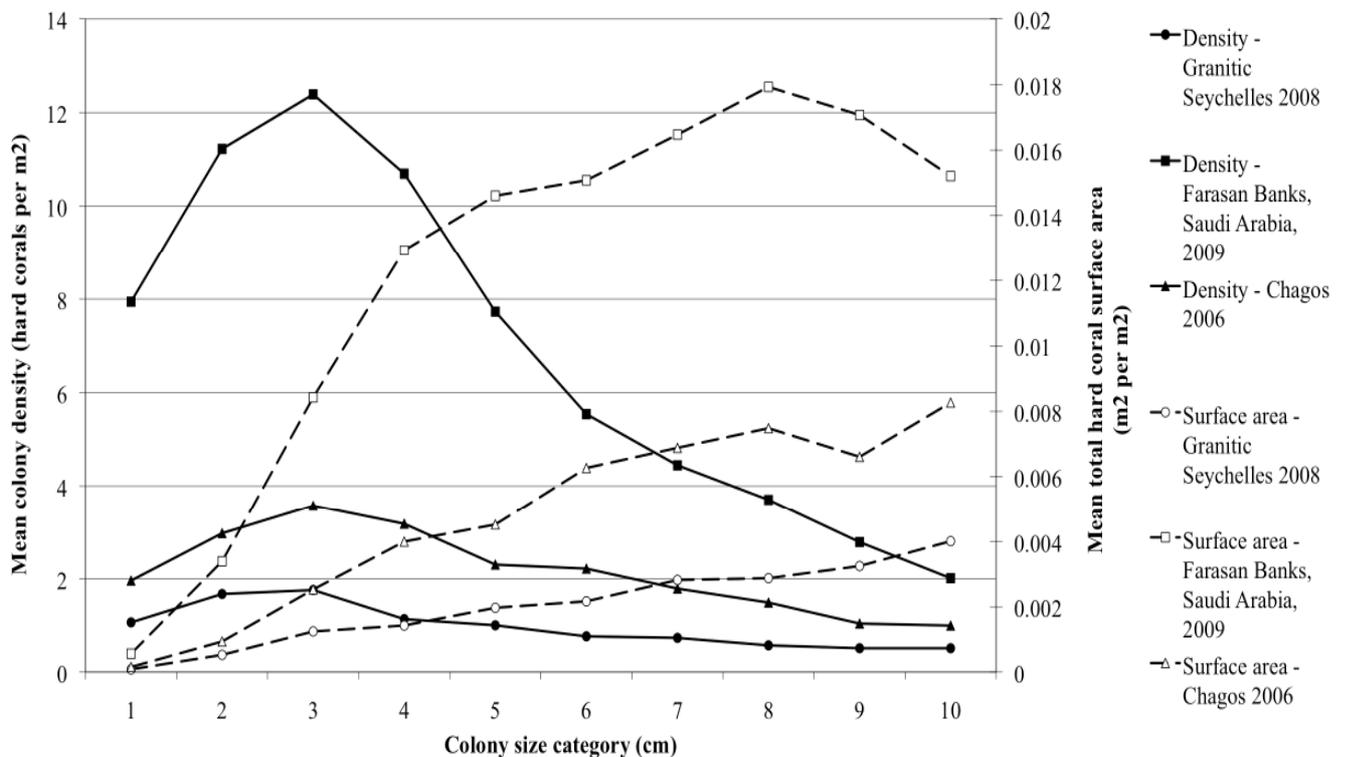


Figure 21. Total number and total surface area of juvenile colonies per size class (all taxa), per 100 m², with comparative data from other Indian Ocean regions (mean of all sites, colonies ≤ 10 cm maximum diameter)

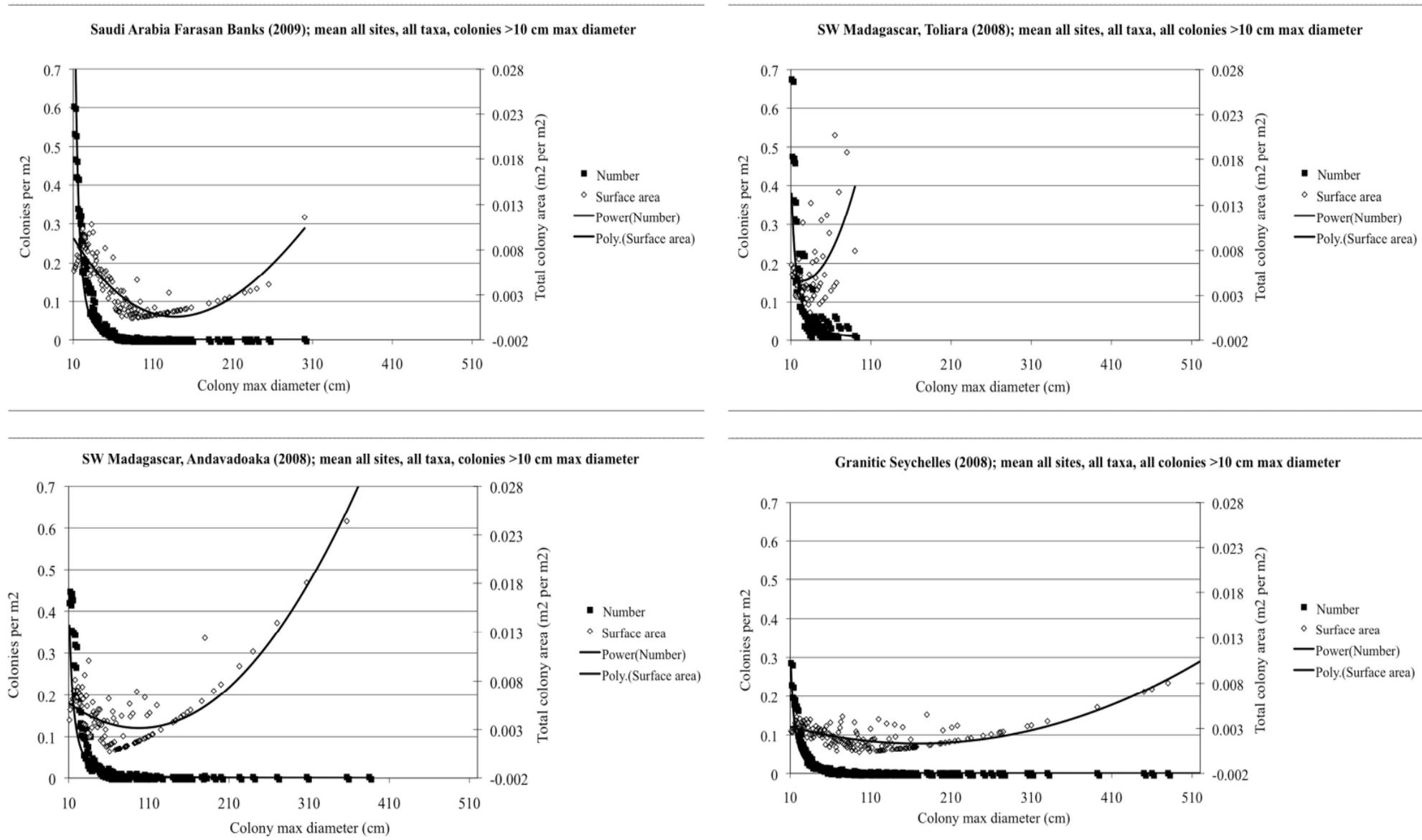


Figure 22. Total number and total surface area of adult colonies per size class, per m² (mean of all sites, colonies > 10 cm maximum diameter)

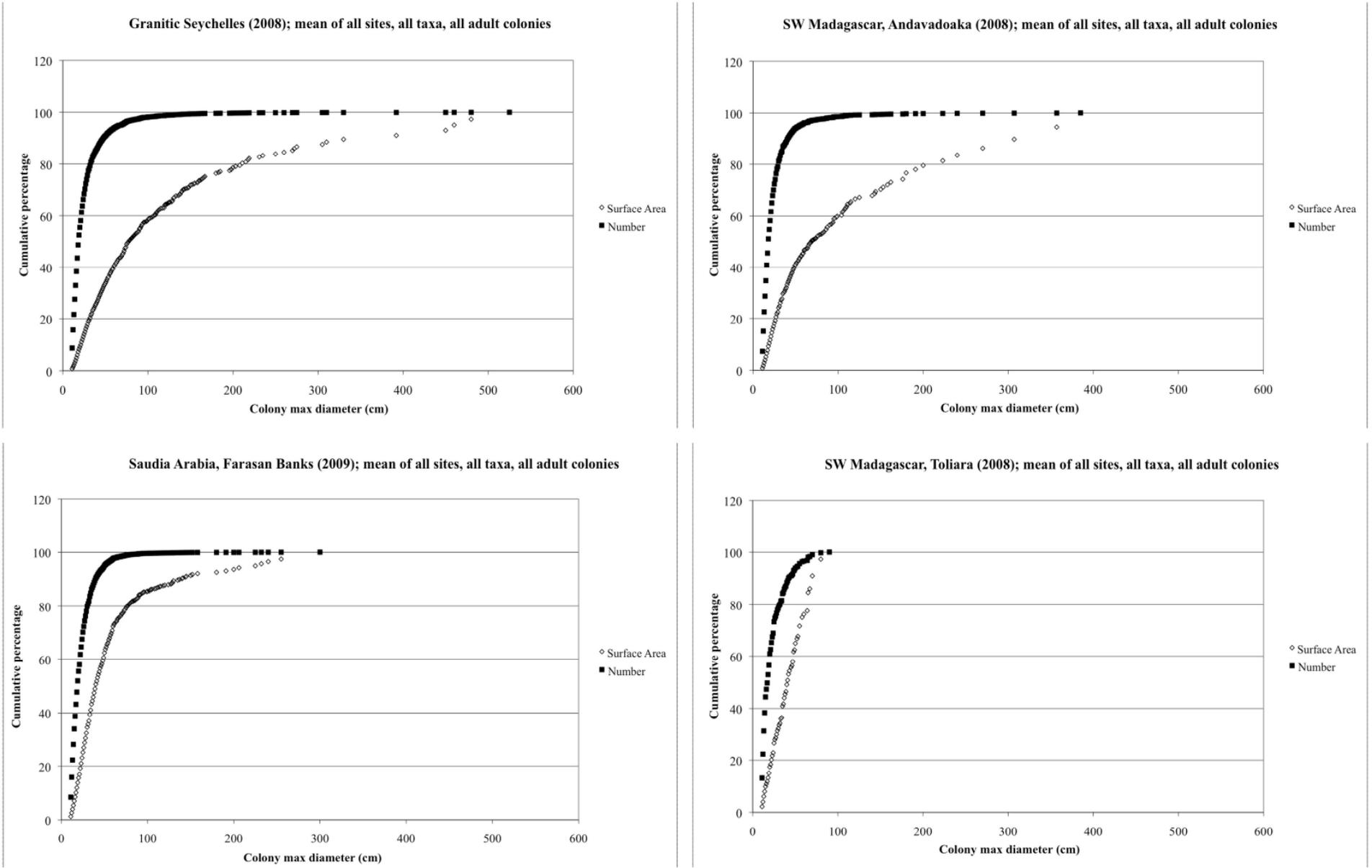


Figure 23. Cumulative percentage adult colony abundance and total adult colony surface area: mean by region, across all adult colony size categories

Despite the differences in curve shape, Figure 22 emphasises the observations drawn from Figure 20; namely that there is a disproportionately large contribution of a small number of large colonies to the total surface area of corals within the reef community. These data also emphasise important life history processes within the coral community, such as the extent to which coral survivorship increases with colony size, as mortality rates decrease.

Across each size category (1 cm increments in maximum colony diameter), differences in adult colony abundance and surface area between regions are, on the whole, proportionately far lower than is seen for juveniles. However the shape of the adult size frequency distribution curve, in particular the upper size limit of coral communities, differs greatly between the four regions for which high-resolution data are available, showing up to 5-fold differences in the range of adult coral community size structure between regions.

The more detailed plots permit much greater understanding of the structure of adult colony communities than is possible from binned or total pooled colony density data alone (Figure 17). For example, while surveys from Toliara recorded approximate 'mid-range' values for adult colony density broadly similar to other regions (Figure 17), Figure 22 shows that the size structure of the coral community in this region is dramatically different to all other regions surveyed, being comprised exclusively of small size classes below 100 cm – an upper size limit less than 1/5 of the maximum size of colonies in the Granitic Seychelles.

Across all colonies surveyed in each region, median adult coral sizes were 18 cm for both Madagascar regions and 19 cm for the Granitic Seychelles and Farasan Banks. In other words half of the adult corals surveyed across all regions were 19 (or 20 cm) or larger, and half were between 11 and 18 (or 19 cm) maximum diameter (Figure 23). Conversely, in terms of contribution to the total surface area of the coral community, the colony size accounting for half of the cumulative surface area of colonies varied considerably, from 40 cm (Farasan Banks, Saudi Arabia) to 78 cm (Granitic Seychelles) (Figure 23).

This indicates that, although small colonies (between 11 and 18 or 19 cm) dominated adult coral communities (accounting for half of the adult corals across all regions), the abundance and distribution of larger colonies greater than 18 or 19 cm, contributing disproportionately to total colony surface area, varied greatly between regions.

The Granitic Seychelles recorded the broadest distribution of colony sizes, with a maximum colony size of 525 cm. This was followed (in order of decreasing maximum colony size) by Andavadoaka, southwest Madagascar (385 cm), Farasan Banks (300 cm), and Toliara, southwest Madagascar (90 cm).

The Farasan Banks, Saudi Arabia, showed the highest colony density across all size classes but a notably depressed size frequency distribution relative to other regions; the colony size accounting for half the cumulative adult coral surface area was below that recorded in Toliara. This indicates that, despite having an extremely high density of corals, the size frequency distribution at the Farasan Banks was composed of predominantly small colonies, with relatively far fewer larger corals than at Toliara. Values of colony size at the 80th percentile of cumulative hard coral surface area emphasise these inter-regional differences in size frequency distribution (Table 4).

Table 4. Colony size characteristics (corals >10 cm maximum diameter) across study regions (pooled taxa)

Survey Region	Colony maximum diameter (cm)					
				Cumulative adult colony surface area		
	Max. adult colony size	Median adult colony size	Mean adult colony size (\pm SE)	Colony size at 20 th percentile	Colony size at 50 th percentile	Colony size at 80 th percentile
Farasan Banks	300	18	23.6 (\pm 0.2)	22	40	76
Granitic Seychelles	525	18	26.8 (\pm 0.3)	31	78	208
Madagascar Toliara	90	19	22.9 (\pm 0.7)	22	41	65
Madagascar Andavadoaka	385	19	24.6 (\pm 0.5)	26	70	200

The cumulative percentage colony abundance and surface area data shown in Figure 23 can also be plotted for the coarser colony size bins from CCCR studies. Figure 24 shows cumulative size frequency distributions from CCCR regions plotted alongside data derived from this study, with adult and juvenile colony data pooled to enable direct comparison of the five coral communities for which both adult and juvenile data are available.

This shows that, across all regions, juvenile colonies account for between 61% (NW Madagascar) and 90% (Farasan Banks) of total colony numerical abundance, but this equates to between only 2% (northwest Madagascar) and 20% (Saudi Arabia Farasan Banks) of total colony surface area (Figure 24). This also emphasises the differences in large colony abundance between the regions; colonies greater than 80cm account for only 6% of the cumulative surface area of colonies in the Farasan Banks, compared to 25% and 30% of the cumulative colony surface area in the Granitic Seychelles and the Outer Seychelles (Amirantes) respectively.

Figure 25 illustrates the differences between the cumulative percentage colony abundance and surface area curves from Figure 24, plotted for each region. On this plot, more positively-skewed curves (i.e. those with a longer right tail, where the main distribution is concentrated on the left of the figure) represent communities with a relatively smaller proportion of large corals; communities at which the distance between the cumulative abundance and area curves in Figure 24 is at its highest at lower colony size categories. This is true of both Saudi Arabian survey regions. The curves for both Seychelles regions, however, show a more symmetrical bell-shaped distribution around the 9 colony size classes, having a relatively higher proportion of larger colonies.

Mean adult colony size differed significantly between regions, from 22.9 ± 0.7 cm SE maximum diameter in Toliara Madagascar to 26.8 ± 0.3 cm SE in the Granitic Seychelles (ANOVA $p < 0.01$).

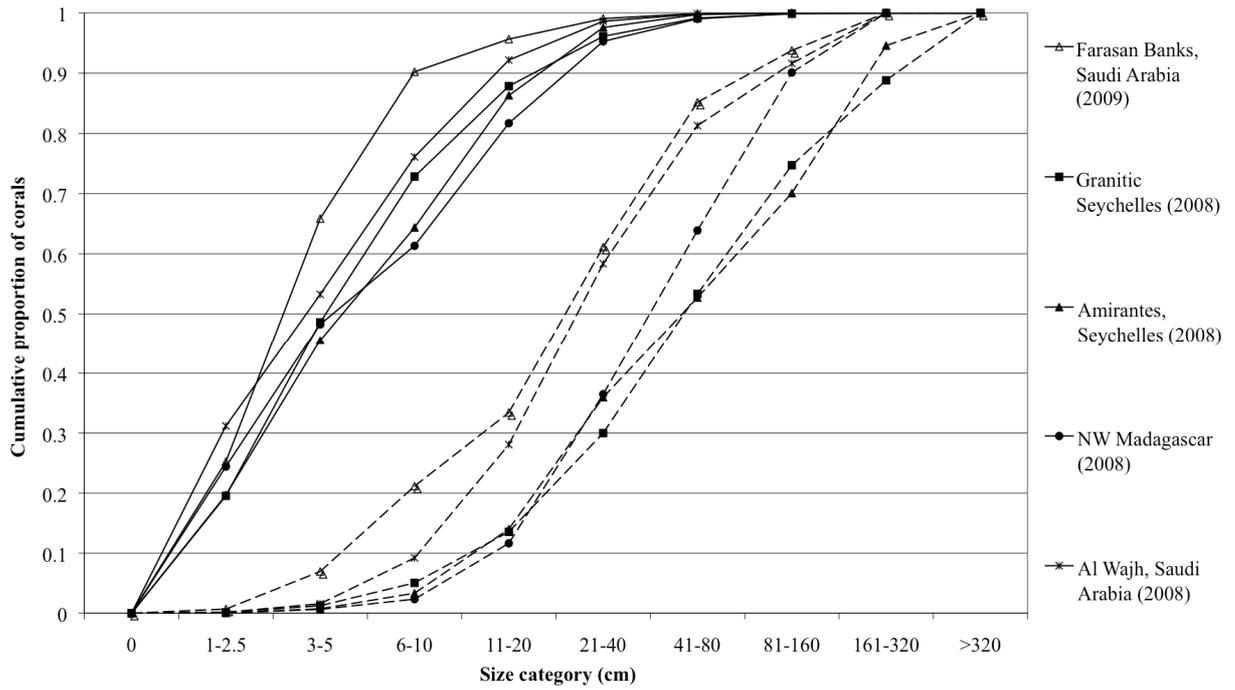


Figure 24. Cumulative percentage colony abundance (solid line) and surface area (broken line) for five survey regions, data pooled by CCCR colony size categories

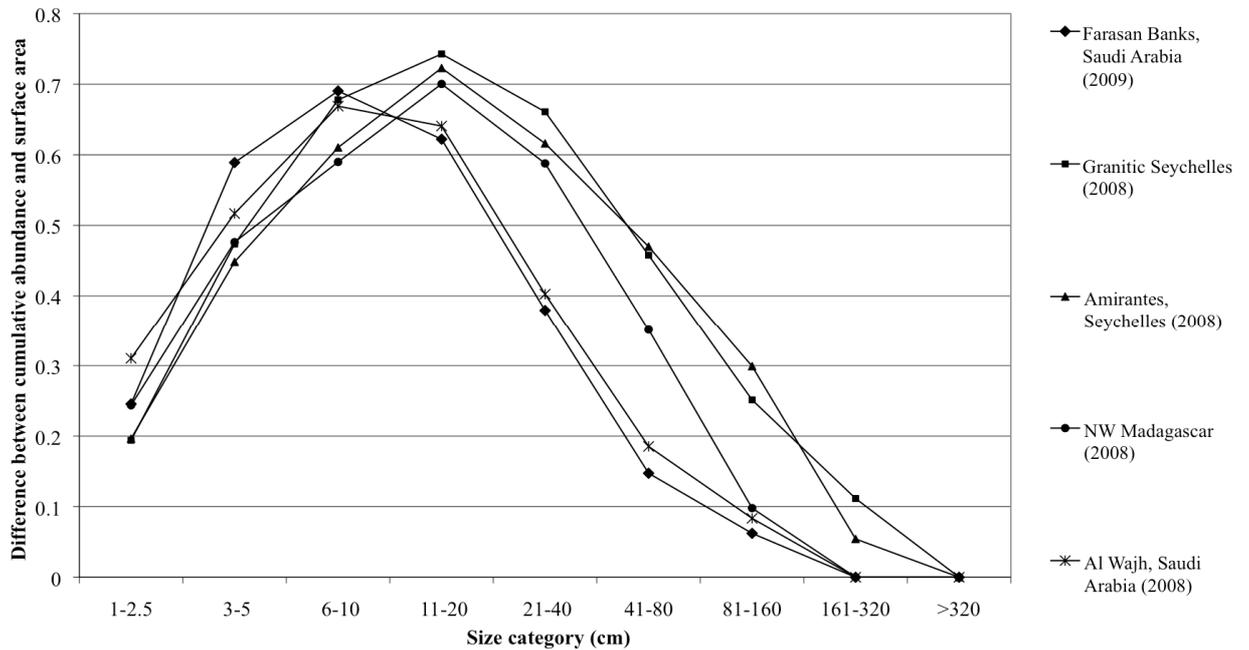


Figure 25. Difference between cumulative proportion curves (colony abundance minus surface area) for each survey region shown in Figure 24

7.1.2.2 Within-region differences

Within the Farasan Banks, analysis of differences in coral community size showed mean colony size to vary with disturbance. Mean adult colony size was lower at sites that had experienced severe mortality than at unaffected sites (20.1 ± 0.3 cm SE maximum diameter compared to 24.2 ± 0.2 cm SE; ANOVA $p < 0.01$). This observation is consistent with multivariate analyses (see section 7.5.1.2; page 133), showing that disturbed depauperate sites in the Farasan Banks had a lower abundance of larger colonies and a higher abundance of juvenile colonies compared to un-impacted reefs.

In contrast to this, in the Granitic Seychelles comparison of mean adult colony sizes per site showed that the granitic sites – those with the highest abundance of adult colonies – exhibited far lower mean colony sizes per site than reef sites based on non-granitic substrata, which were generally considerably more depauperate than the granitic reefs (23.3 ± 0.3 cm SE maximum diameter compared to 28.9 ± 0.6 cm SE and 31.7 ± 0.9 cm for patch and carbonate reefs respectively; ANOVA $p < 0.01$).

7.2 Coral populations; summary statistics and graphical representations for individual genera

This section presents summary statistics and graphical interpretations of coral population data collected from the five reef regions visited in this research, describing between and within region differences in colony density, surface area, and size frequency distributions for individual genera and families of adult corals.

7.2.1 Colony density and total colony surface area (individual taxa)

Figure 26 shows the between-region variation in absolute and relative values of colony density and surface area for adult corals from the 21 most dominant genera (dominance ranked in terms of contribution to total colony surface area for all 4 survey regions for which adult coral data are available). These plots show the far higher dominance of *Porites* at the Granitic Seychelles and Farasan Banks compared to other regions.

Toliara shows the least similarity to other regions, with much lower relative abundance of *Porites* and *Acropora*, and higher relative surface area of taxa that are elsewhere subordinate.

Plots in Figure 27 to Figure 29 follow the same treatment as Figure 26, illustrating within-region differences in relative dominance of genera, with values grouped by different factors under analysis. Three regions permit analyses of within region differences using similar treatments:

Within the Granitic Seychelles the three geomorphological classes of reef are separated (Figure 27). Corals on granitic substrata are the most dissimilar, with much higher colony abundance and surface area for most taxa. These sites also show much higher relative numerical dominance of *Favites*, *Acropora*, *Pocillopora* and *Diploastrea*, and lower relative and absolute surface area of *Porites*.

Within the Farasan Banks the methods show the differences between sites exposed to the three levels of observed mortality (Figure 28). Here, absolute abundance and surface area of most taxa decreases with increasing severity of coral mortality. Relative abundance of *Porites* is higher at sites exposed to severe mortality. *Pocillopora*, *Galaxea*, *Goniopora*, and *Millepora* also show relatively higher values of colony abundance and/or surface area in severely affected sites. Conversely the relative abundance and surface area of *Acropora*, *Montipora*, *Echinopora* and *Stylophora* were lower at severely affected sites.

In Andavadoaka similarly, differences between protected and unprotected sites are clear (Figure 29). Here, protected sites show markedly higher absolute and relative abundance and surface area of *Echinopora*, *Porites*, *Acropora*, *Montipora* and *Pocillopora*. Unprotected sites show lower absolute values for most taxa, but higher relative abundance and surface area of *Diploastrea*, *Favia*, *Favites*, *Goniastrea*, *Goniopora*, *Pachyseris*, *Astreopora*, *Hydnophora* and four other faviid genera.

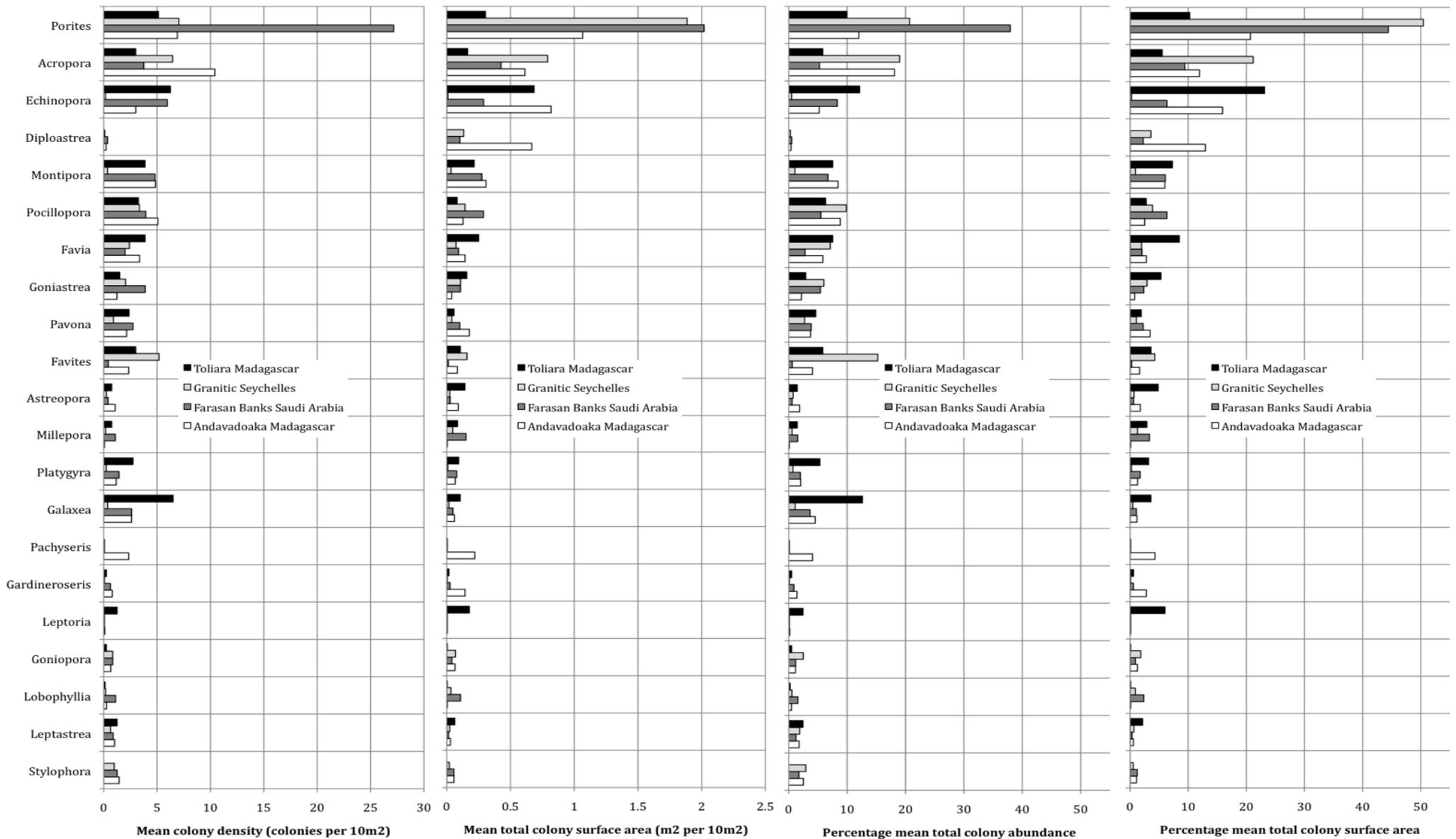


Figure 26. Adult colony density (corals per 10m²) and surface area (m² per 10 m²) of dominant scleractinian genera by region, showing absolute values (left and centre left) and relative values (right and centre right) in each case. Taxa ordered by sum of absolute coral surface area (across all regions)

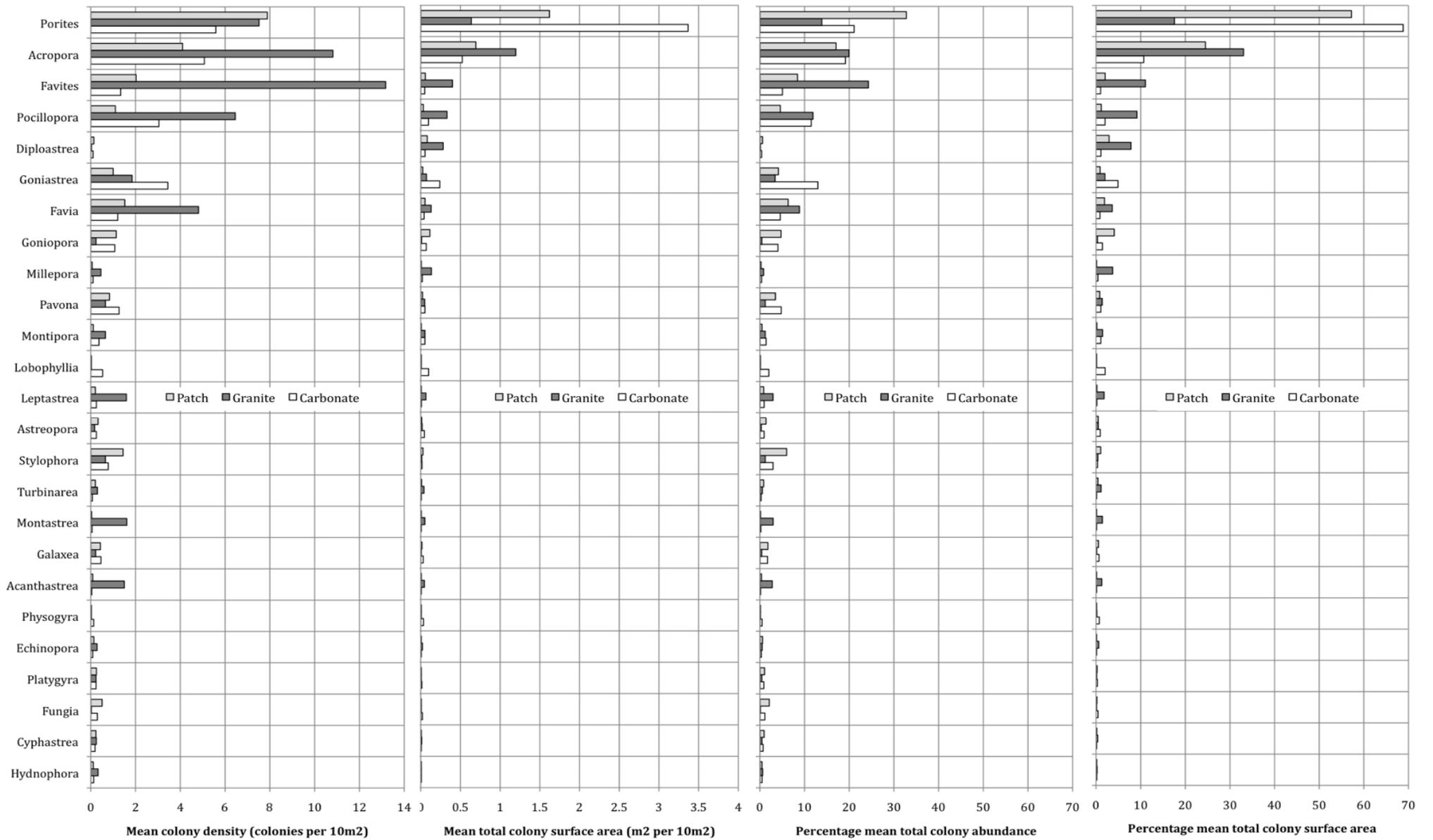


Figure 27. Adult colony density and surface area for dominant scleractinian genera at the Granitic Seychelles, showing absolute values (left and centre left) and relative values (right and centre right). Sites grouped by geomorphological reef type (Jennings 1996). Taxa ordered by sum of absolute coral surface area (across all reef types)

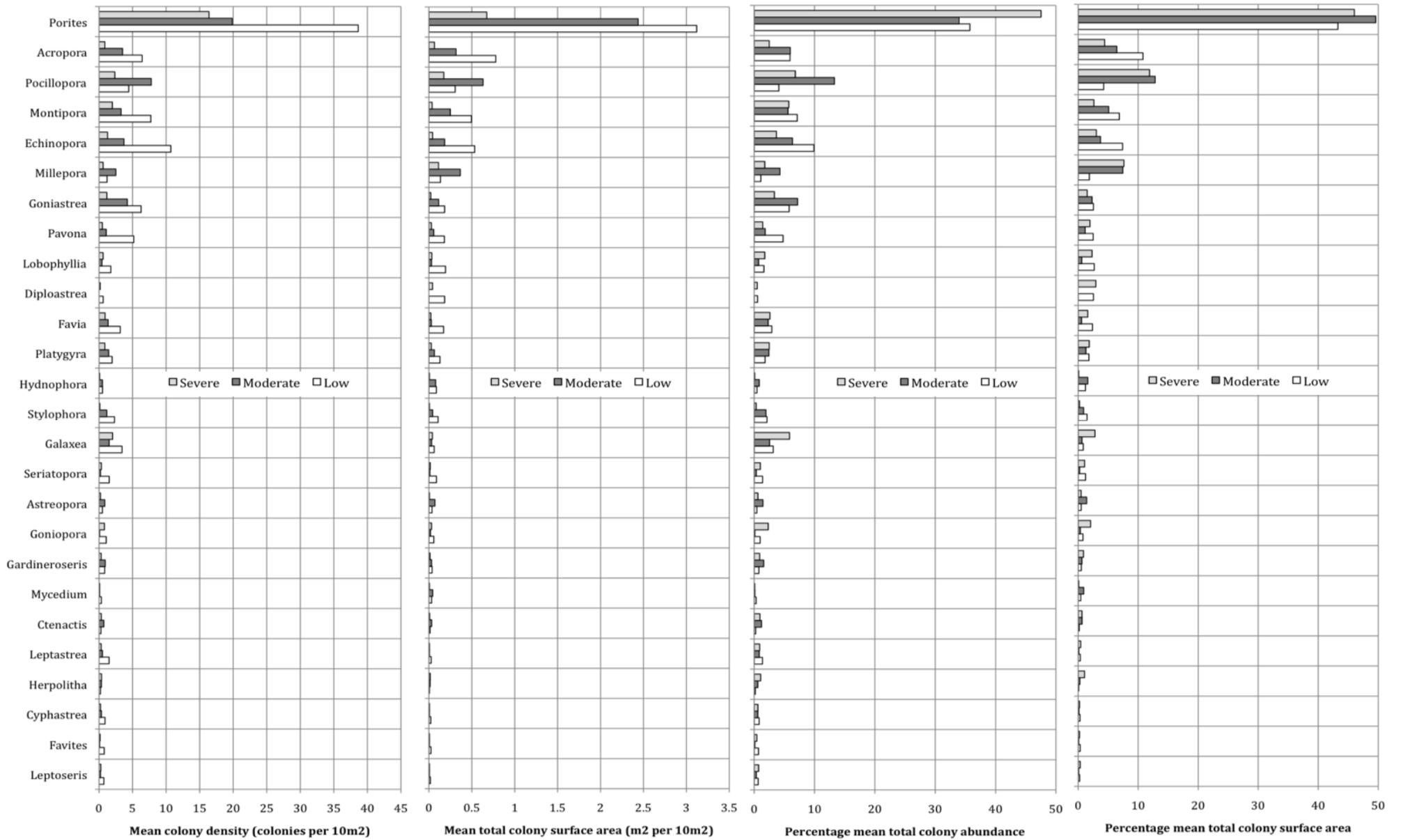


Figure 28. Adult colony density and surface area of dominant genera at the Farasan Banks, Saudi Arabia, showing absolute values (left and centre left) and relative values (right and centre right) in each case. Sites grouped by the degree of observed mortality. Taxa ordered by sum of absolute coral surface area (across all categories)

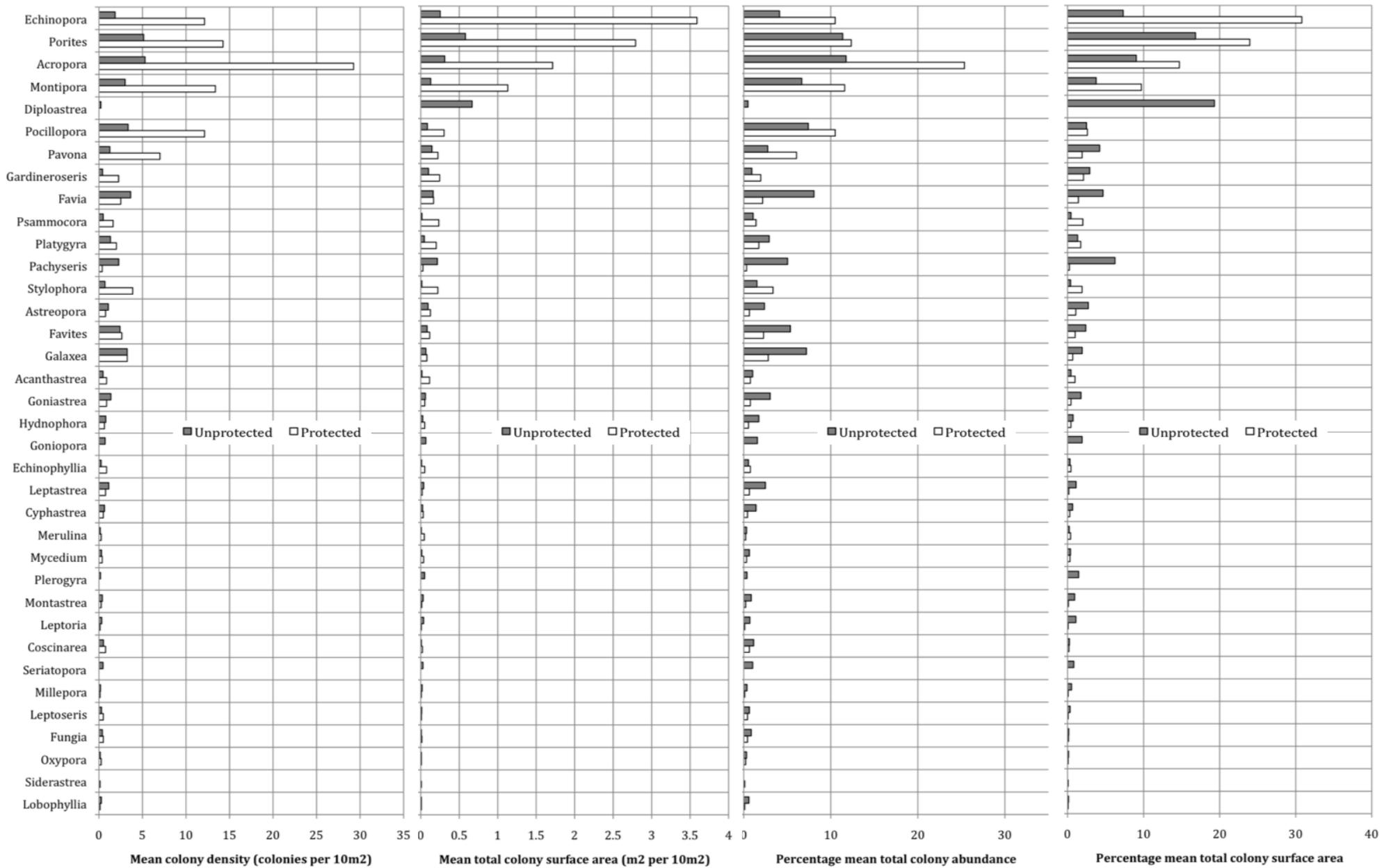


Figure 29. Adult colony density and surface area of dominant scleractinian genera at Andavadaoaka, Madagascar, showing absolute values (left and centre left) and relative values (right and centre right) in each case. Sites grouped by management. Taxa ordered by sum of absolute coral surface area (across both categories)

Examination of the dominant juvenile and adult families for all eight regions shows the broad dominance of Faviidae and Poritidae (Table 5), in terms of both area and abundance for all survey regions (including CCCR regions), while available comparable juvenile data from the Arabian Seas in 2002 (Figure 30) shows broadly similar patterns at family level (Wilson 2007).

Table 5 - dominant hard coral families in juvenile and adult communities, by relative abundance and surface area, by region

	Colony size	Dominant family	
		Colony density	Total colony area
Farasan Banks Saudi Arabia	≤10cm	Poritidae	Faviidae
	>10cm	Poritidae	Poritidae
Granitic Seychelles	≤10cm	Faviidae	Faviidae
	>10cm	Faviidae	Poritidae
Outer Seychelles	≤10cm	Faviidae	Faviidae
	>10cm	Poritidae	Poritidae
Madagascar Nosy Hara	≤10cm	Acroporidae	Acroporidae
	>10cm	Acroporidae	Acroporidae
Al Wajh Saudi Arabia	≤10cm	Poritidae	Poritidae
	>10cm	Poritidae	Acroporidae
Chagos	≤10cm	Agariciidae	Agariciidae
Madagascar Andavadoaka	>10cm	Acroporidae	Faviidae
Madagascar Toliara	>10cm	Faviidae	Faviidae

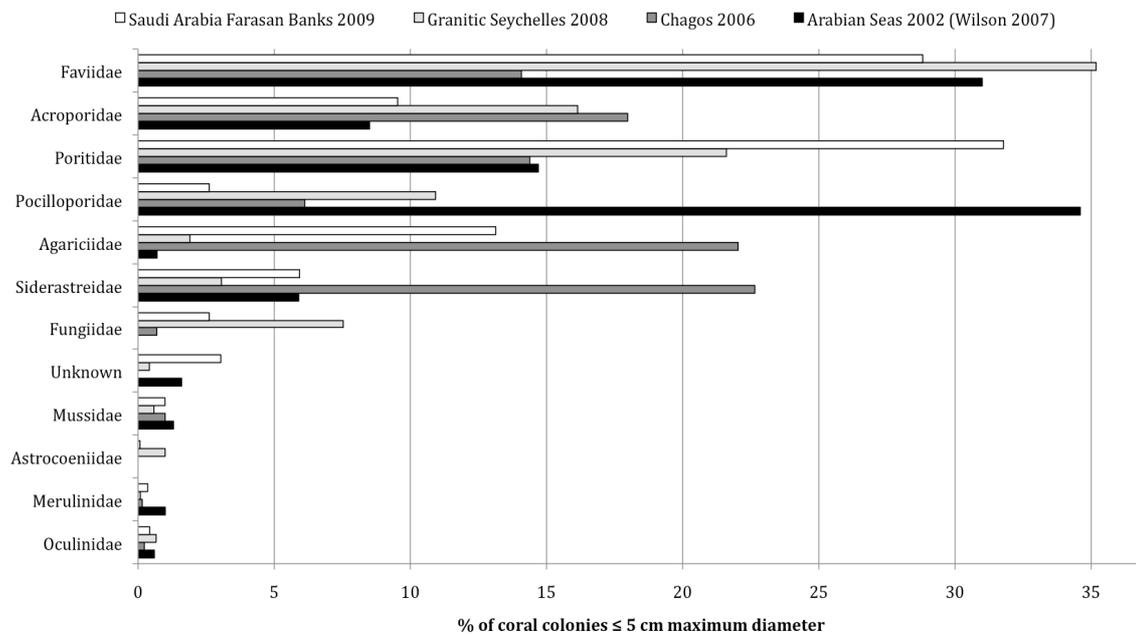


Figure 30. Relative abundance of juvenile colonies across all survey regions for which juvenile data were collected. Data are based only on colonies ≤5 cm maximum diameter to enable comparison with values from Wilson (2007)

7.2.2 Colony size frequency distribution (individual taxa)

Figure 31 and Figure 32 illustrate the contributions of the six most dominant scleractinian families (in terms of surface area and colony density) to the size frequency distribution plots shown in Figure 19 and Figure 20 (section 7.1.2). These size-based representations of coral communities provide a clear depiction of the changing contribution of different taxa across different size classes and illustrate major differences between regions.

At family level there are pronounced differences between taxa, but numerical dominance of a taxon is not necessarily related to area dominance. For example, the absolute abundance and surface area of juvenile colonies from the families Poritidae and Faviidae at the Farasan Banks is so great relative to other regions that their total juvenile colony density and surface area is approximately double that of the combined values of all taxa from the Granitic Seychelles (Figure 31). Similarly, the total density of corals at Nosy Hara (all taxa and sizes) is less than the colony density of four individual coral families in the Farasan Banks (Poritidae, Faviidae, Agariciidae and Acroporiidae) (Figure 32; page 117 and Table 6; page 115).

The scale of these differences in absolute values of colony density and total colony surface area between regions prevents direct visual comparison of depauperate regions against richer regions on the same arithmetical scale. However, standardisation of these values (Figure 33 and Figure 34) enables direct comparison of relative colony abundance and surface area, across all colony size classes.

For example, the relative dominance of juvenile Poritidae and Faviidae over other taxa in the Farasan Banks and Granitic Seychelles (Figure 33) contrasts with Chagos, where Acroporidae, Siderastreidae and especially Agariciidae are prominent. In contrast, overall coral surface area is dominated by Poritidae at both Saudi Arabian regions and the Granitic Seychelles (Figure 34).

There are marked differences too in relative contribution of Acroporidae to the overall coral surface area; from the Outer Seychelles where Acroporidae comprise just 4% of colony area to Nosy Hara, Madagascar where they comprise 51% (Table 7; page 115).

The Granitic Seychelles showed the highest proportion of total coral colony surface area in the highest colony size class (>320cm) of all regions surveyed, including the comparative CCCR survey regions (11% of total colony surface area; more than twice that in the second highest region for this size class, namely the Granitic Seychelles). The large colonies contributing to the high cover were predominantly Poritidae. The Granitic Seychelles also showed more than twice the relative total surface area of corals of the Farasan Banks in the second and third highest colony size classes.

These figures illustrate the profoundly different conclusions that may be drawn from interpreting colony abundance versus surface area data. Whereas in terms of colony density, Faviids dominated both the adult and juvenile coral communities at the Granitic Seychelles, followed by (in order of decreasing abundance) poritids, acroporids and pocilloporids (Figure 32; Table 6), total surface area of adults was dominated by poritids, followed by acroporids then faviids (Figure 34; Table 7). Conversely, within the juvenile coral community, surface area is dominated by faviids, followed by acroporids and poritids.

Data presented in Figure 31 to Figure 34 are summarised in Table 6 and Table 7.

Table 6. Mean colony density for adult and juvenile colonies; colonies per 100 m² (and % of total, adults and juveniles combined). Dominant families in each region are highlighted

Region	Size	Acroporidae	Pocilloporidae	Agaricidae	Favidae	Poritidae	Siderastreidae	Other	Total
Farasan Banks Saudi Arabia <i>(Harris 2009)</i>	≤10cm	692 (9%)	160 (2%)	856 (12%)	1957 (27%)	1991 (27%)	402 (5%)	556 (8%)	6614 (90%)
	>10cm	90 (1%)	61 (1%)	39 (1%)	158 (2%)	280 (4%)	4 (0%)	86 (1%)	717 (10%)
Granitic Seychelles <i>(Harris 2008)</i>	≤10cm	139 (12%)	97 (8%)	24 (2%)	315 (27%)	168 (14%)	24 (2%)	89 (8%)	856 (73%)
	>10cm	64 (6%)	40 (3%)	9 (1%)	105 (9%)	72 (6%)	1 (0%)	19 (2%)	310 (27%)
Outer Seychelles <i>(Obura 2008)</i>	≤10cm	89 (5%)	209 (11%)	153 (8%)	350 (19%)	338 (18%)	2 (0%)	35 (2%)	1176 (64%)
	>10cm	41 (2%)	107 (6%)	67 (4%)	168 (9%)	260 (14%)	4 (0%)	5 (0%)	652 (36%)
Madagascar Nosy Hara <i>(Obura 2008)</i>	≤10cm	129 (17%)	108 (14%)	5 (1%)	83 (11%)	111 (14%)	6 (1%)	28 (4%)	470 (61%)
	>10cm	131 (17%)	47 (6%)	24 (3%)	49 (6%)	36 (5%)	2 (0%)	16 (2%)	305 (39%)
Al Wajh Saudi Arabia <i>(Obura 2008)</i>	≤10cm	520 (11%)	351 (7%)	285 (6%)	736 (15%)	1611 (34%)	15 (0%)	115 (2%)	3633 (76%)
	>10cm	317 (7%)	135 (3%)	44 (1%)	211 (4%)	367 (8%)	8 (0%)	45 (1%)	1127 (24%)

Table 7. Mean colony surface area for adult and juvenile colonies; m² per 100 m² (and % of total, adults and juveniles combined). Dominant families in each region are highlighted

Region	Size	Acroporidae	Pocilloporidae	Agaricidae	Favidae	Poritidae	Siderastreidae	Other	Total
Farasan Banks Saudi Arabia <i>(Harris 2009)</i>	≤10cm	1.4 (2%)	0.2 (0%)	1.6 (3%)	3.7 (6%)	3.4 (6%)	0.8 (1%)	1.1 (2%)	12.2 (21%)
	>10cm	7.3 (13%)	3.9 (7%)	1.4 (2%)	7.3 (13%)	20.6 (36%)	0.1 (0%)	4.7 (8%)	45.5 (79%)
Granitic Seychelles <i>(Harris 2008)</i>	≤10cm	0.3 (1%)	0.2 (1%)	0.1 (0%)	0.7 (2%)	0.3 (1%)	0.0 (0%)	0.2 (0%)	1.9 (5%)
	>10cm	7.7 (22%)	1.5 (4%)	0.4 (1%)	5.0 (14%)	17.8 (50%)	0.0 (0%)	1.5 (4%)	34.0 (95%)
Outer Seychelles <i>(Obura 2008)</i>	≤10cm	0.1 (0%)	0.2 (0%)	0.3 (1%)	0.8 (1%)	0.7 (1%)	0.0 (0%)	0.1 (0%)	2.2 (3%)
	>10cm	2.8 (4%)	4.4 (7%)	11.1 (17%)	16.1 (24%)	29.1 (44%)	0.3 (0%)	0.4 (1%)	64.3 (97%)
Madagascar Nosy Hara <i>(Obura 2008)</i>	≤10cm	0.2 (1%)	0.1 (0%)	0.0 (0%)	0.2 (1%)	0.2 (0%)	0.0 (0%)	0.0 (0%)	0.7 (2%)
	>10cm	16.7 (51%)	1.8 (6%)	2.2 (7%)	5.2 (16%)	5.3 (16%)	0.1 (0%)	0.7 (2%)	32.1 (98%)
Al Wajh Saudi Arabia <i>(Obura 2008)</i>	≤10cm	1.2 (2%)	0.6 (1%)	0.5 (1%)	1.5 (2%)	2.5 (4%)	0.0 (0%)	0.3 (0%)	6.7 (9%)
	>10cm	25.6 (35%)	5.8 (8%)	1.5 (2%)	8.0 (11%)	22.4 (31%)	0.3 (0%)	2.2 (3%)	65.9 (91%)

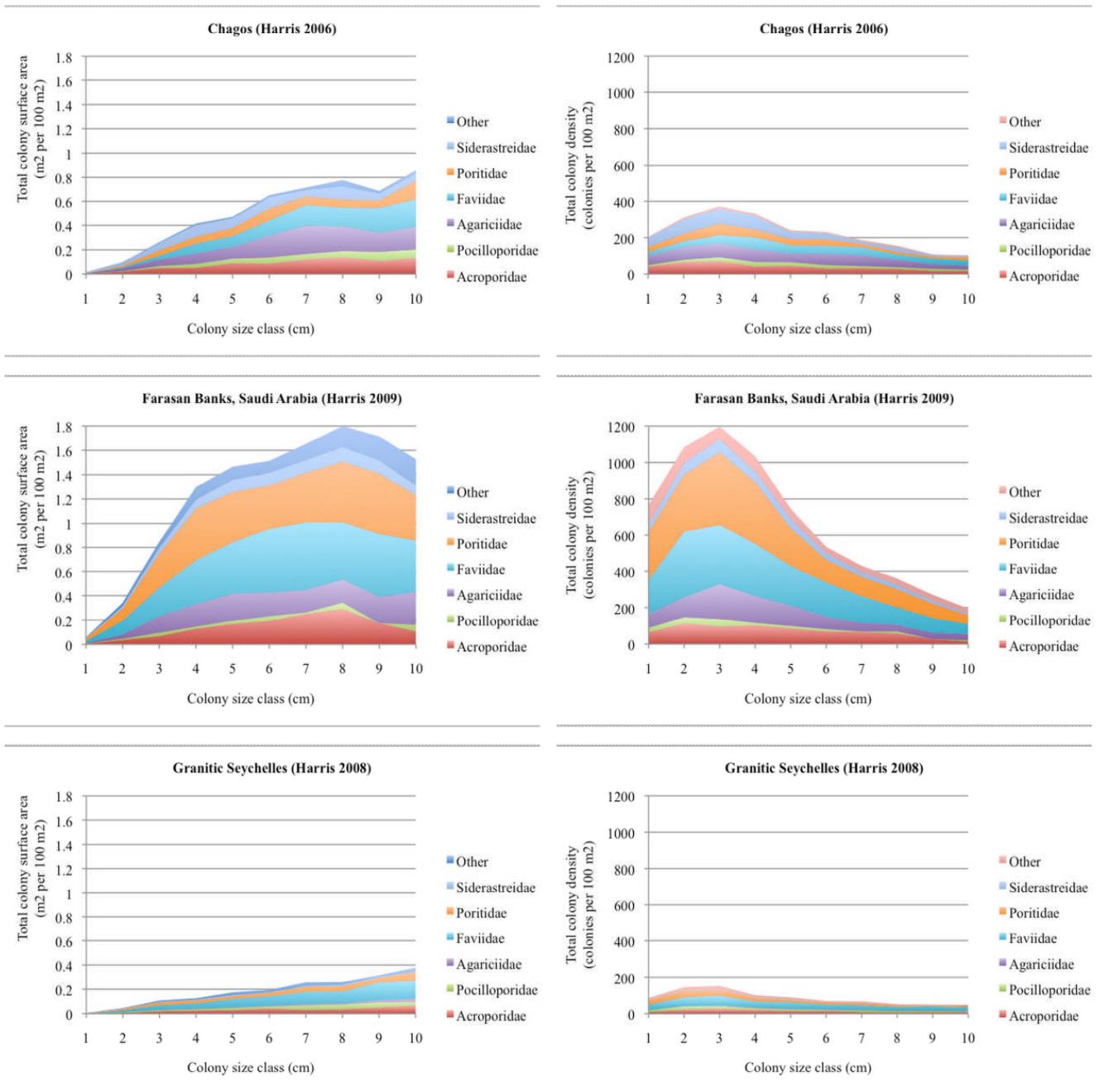


Figure 31. Contribution of dominant scleractinian families to juvenile hard coral size frequency distribution, based on total colony surface area (left) and colony density (right), values represent mean based on all transects for each region

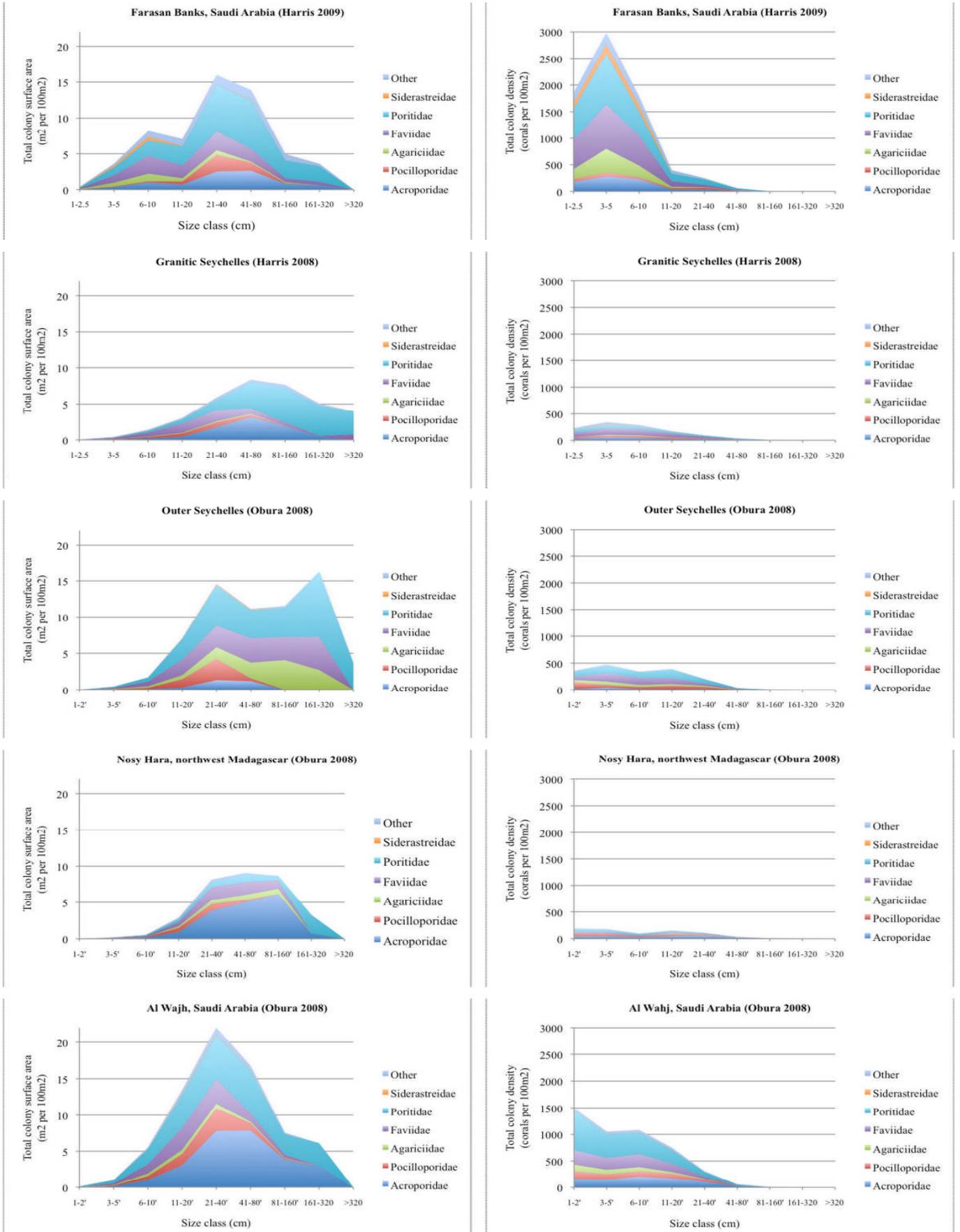


Figure 32. Contribution of dominant scleractinian families to adult hard coral size frequency distribution, based on total colony surface area (left) and colony density (right), values represent mean based on all transects for each region

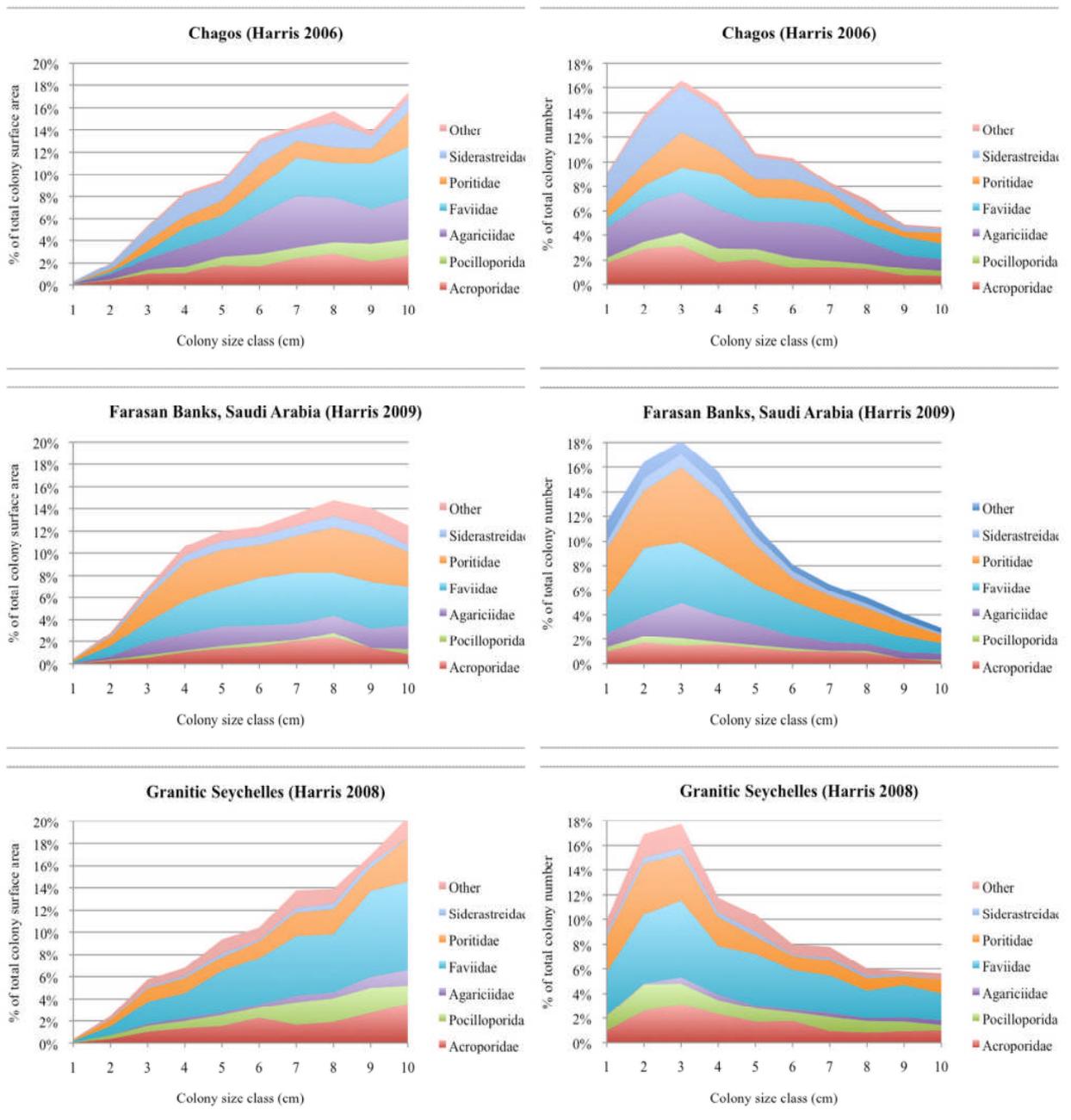


Figure 33. Relative contribution of dominant scleractinian families to juvenile hard coral size frequency distribution, based on total colony surface area (left) and colony density (right), values represent mean based on all transects for each region

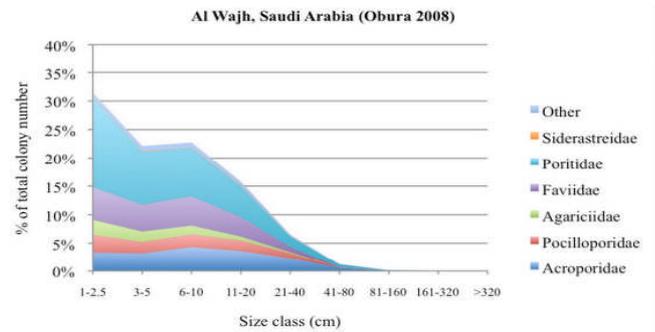
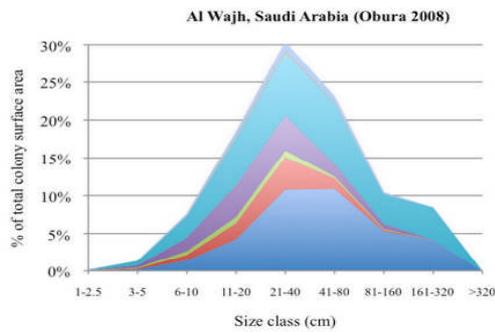
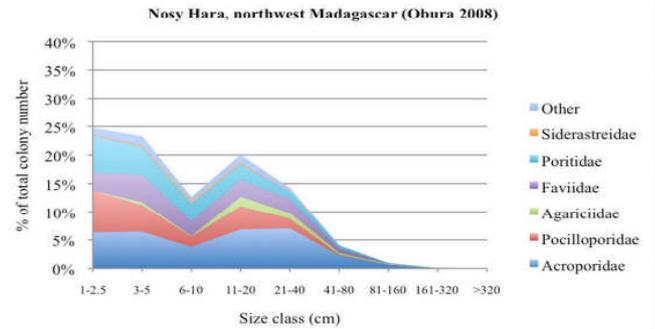
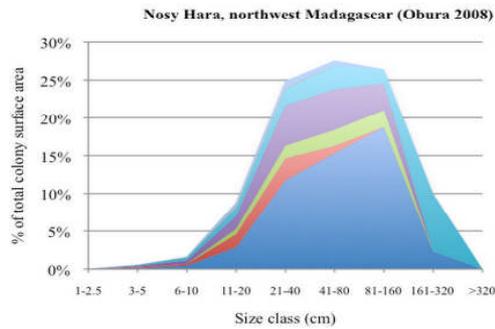
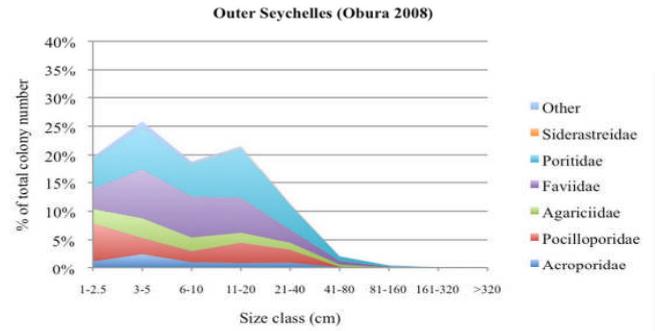
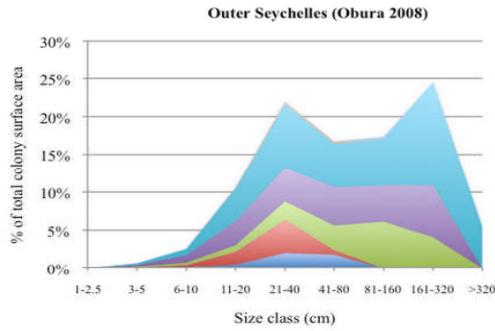
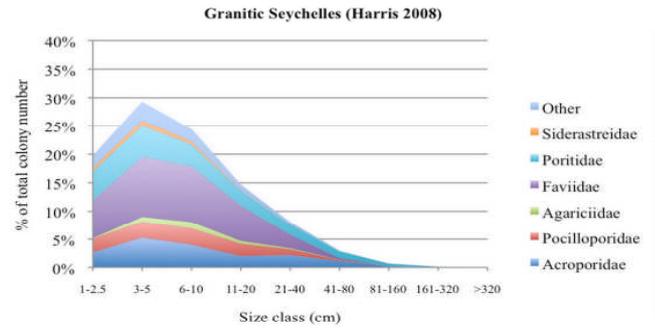
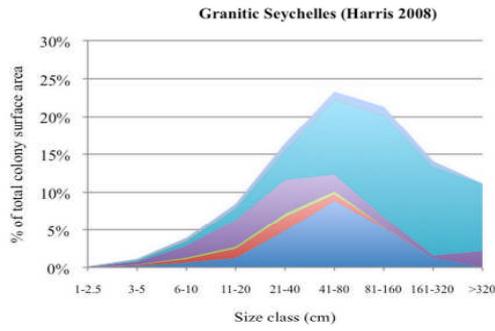
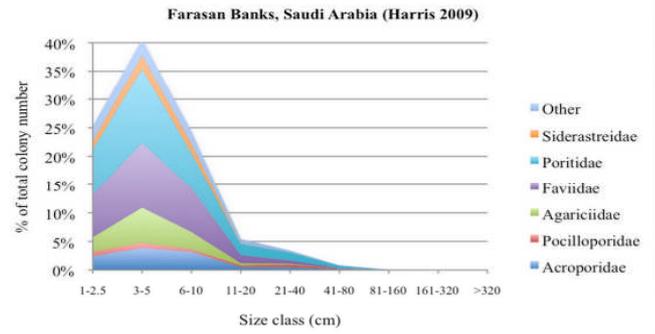
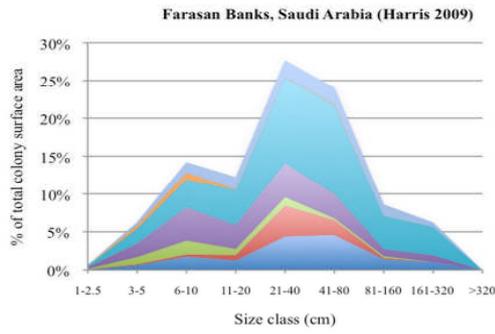


Figure 34. Relative contribution of dominant scleractinian families to hard coral size frequency distribution (adult and juvenile data combined), based on total colony surface area (left) and colony density (right), values represent mean based on all transects for each region

7.2.3 Size and demographic parameters for individual genera

This section examines differences in demographic parameters of coral populations for individual genera within and between survey regions. Colony size distribution parameters are shown for individual genera from all four survey regions in Appendices 2 and 3.

The arithmetical scale of area data was changed to a geometrical function of colony size by log transformation of values to approximately normalise frequency distributions (Bak and Meesters 1998). These demographic parameters show maximum, minimum, median and mean values of colony diameter and surface area, as well as kurtosis, skewness, and standard error values for all genera across all regions studied. All values are derived from adult colony data only.

Sample sizes varied between taxa, from a minimum of 1 colony per genus per region (for 14 region-specific populations across 4 regions), to a maximum of 3316 colonies per genus population (for *Porites* in the Farasan Banks, Saudi Arabia). This variability inevitably reduces the statistical power and accuracy of analyses based on populations with small sample sizes, although correlation analysis showed no relationship between sample size (number of colonies) per region-specific population mean colony size and any of the demographic parameters under investigation. The mean number of colonies measured per genus for all populations across all four regions was 117 (± 26 SE).

Mean adult colony size varied greatly between taxa and regions (Appendix 2 and Figure 35; page 123). The lowest mean genus size recorded was equal to the lowest possible colony size (11 cm diameter; 0.01 m²) for five genera in three regions: *Alveopora* (Farasan Banks), *Leptoseris* (Granitic Seychelles), and *Lobophyllia*, *Psammocora* and *Symphyllia* (Toliara, Madagascar). The largest mean size was 165 cm \pm 38 SE diameter (equivalent to 3.04 m² \pm 1.22 SE) in *Diploastrea heliopora* in Andavadoaka, Madagascar. The largest colony size recorded was a colony of *Porites lutea* in the Granitic Seychelles, measuring 525 cm diameter; 21.65 m².

The rank order of generic and family sizes also varied considerably between regions (Appendix 2). *Diploastrea* was the largest genus (in terms of mean colony size) in the Farasan Banks and Andavadoaka, whereas *Acropora* and *Plerogyra* showed the largest mean sizes in Toliara and the Granitic Seychelles respectively. In terms of maximum colony size, the order and nature of families also changed between regions, with Faviidae, Acroporidae, Poritidae, Euphyllidae, Merulinidae, and Pocilloporidae all featuring as one of the largest three coral families in one or more regions.

Skewness was positive in 103 of the 109 log-transformed populations analysed across the four 4 regions (based only on populations with 10 or more colonies on which to calculate demographic parameters), which contrasts with observations of negatively-skewed size frequency distributions based on untransformed colony area data from pooled taxa (section 7.1.2; page 96 and Figure 20; page 97), a result of the logarithmic transformation. Negative skewness values were mostly very close to zero, predominantly in uncommon faviid and fungiid genera. Kurtosis distributions were positive (leptokurtotic) in 57 of the 109 populations, indicating that approximately half of the populations showed pointed size distributions around the mean.

Based on logarithmically-transformed area data, mean population size is negatively correlated to population kurtosis and skewness ($r = -0.34$, $p < 0.001$ and $r = -0.55$, $p < 0.001$ respectively, based only on populations consisting of 10 or more colonies)(Figure 37). The highly significant negative correlation between mean size and skewness, across all region-specific genus populations, is explained by the fact that skewness, or asymmetry, reflects the contribution of small versus large colonies to the total population. Thus populations with smaller means (based on log area) are more positively skewed, with relatively fewer larger colonies within the population size frequency distribution. Conversely populations with larger means showed decreased - and eventually negative - skewness, representing a longer left tail of the population distribution, on account of a relatively higher proportion of larger colonies within the size frequency distribution.

Similarly, the cause of the negative relationship between population mean size and kurtosis distributions is likely to be a result of the more truncated size distributions of populations of smaller corals, in which the greater numerical dominance of the smallest colonies (a factor true of all populations, regardless of size distribution) causes a relatively much greater pointed shape to the distribution.

Power analyses carried out on data prior to statistical analysis revealed an insufficient sample size for data collected in the Toliara region to allow between-region testing of genus size frequency distributions. Toliara data recorded lower power than other survey regions because of a comparatively smaller sample size of sites (and therefore total recorded corals) from this region, which resulted in non homogeneous variances of demographic data between Toliara and other survey regions, thus breaking a key assumption of the One Way ANOVA test (Dytham 1998). Therefore data from this region were omitted during parametric statistical analysis.

Appendix IV shows results of ANOVA testing for significance of differences in mean surface areas of adult colonies (>10 cm maximum diameter) from populations of all genera across the three remaining survey regions (Andavadoaka, Granitic Seychelles and Farasan Banks). Despite the large number of replicate surveys carried out many of the genera were too sparsely distributed to carry sufficient power for statistical analysis, or were completely missing from one or more of the regions.

Mean colony surface area values, by region, for all taxa for which significant differences in colony size occurred between regions (ANOVA $p \leq 0.05$), emphasise the distinct inter-regional differences in genus populations (Figure 35). Although significant differences exist in generic population size distributions between regions, there are no consistent trends in these population sizes between regions, and these differences are likely anyway to be strongly influenced by within-genus species differences between regions.

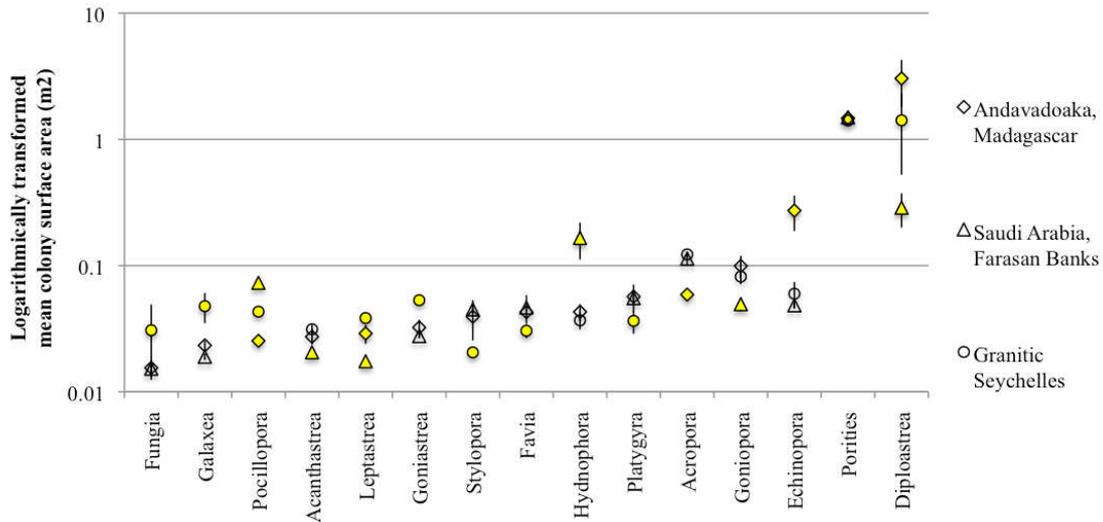


Figure 35. Mean colony size (corals >10cm maximum diameter) by genus (\pm standard error) for three survey regions, showing all genera for which significant differences between regions occur (ANOVA $p \leq 0.05$). Highlighted data points indicated significantly different population means from other regions

Repeating the above procedure to identify within-region differences in genus populations in the Farasan Banks based on the degree of observed mortality identifies (present or absent) shows pronounced differences in genus sizes between sites affected and unaffected by the recent mortality event (Figure 36; page 124).

Appendix IV shows results of two-sample T-tests for significance of differences in mean surface areas of adult colonies (>10 cm maximum diameter) from affected and unaffected sites within the Farasan Banks. Of 42 genera recorded at sites in both categories (presence and absence of reef mortality), 35 showed smaller mean colony sizes at sites showing evidence of mortality (Appendix IV)(Figure 36; page 124). Owing to power constraints from small sample sizes within some taxa not all of these differences could be tested statistically, however of the 11 genera that showed significantly different sizes between affected and unaffected reefs (two sample T-test $p \leq 0.05$) 10 showed larger colony sizes at unaffected reefs, including the three dominant adult taxa in terms of numerical abundance in the Farasan Banks (*Porites*, *Montipora* and *Echinopora*, in order of decreasing abundance). The only genus showing significantly smaller colonies at affected sites was *Pocillopora*.

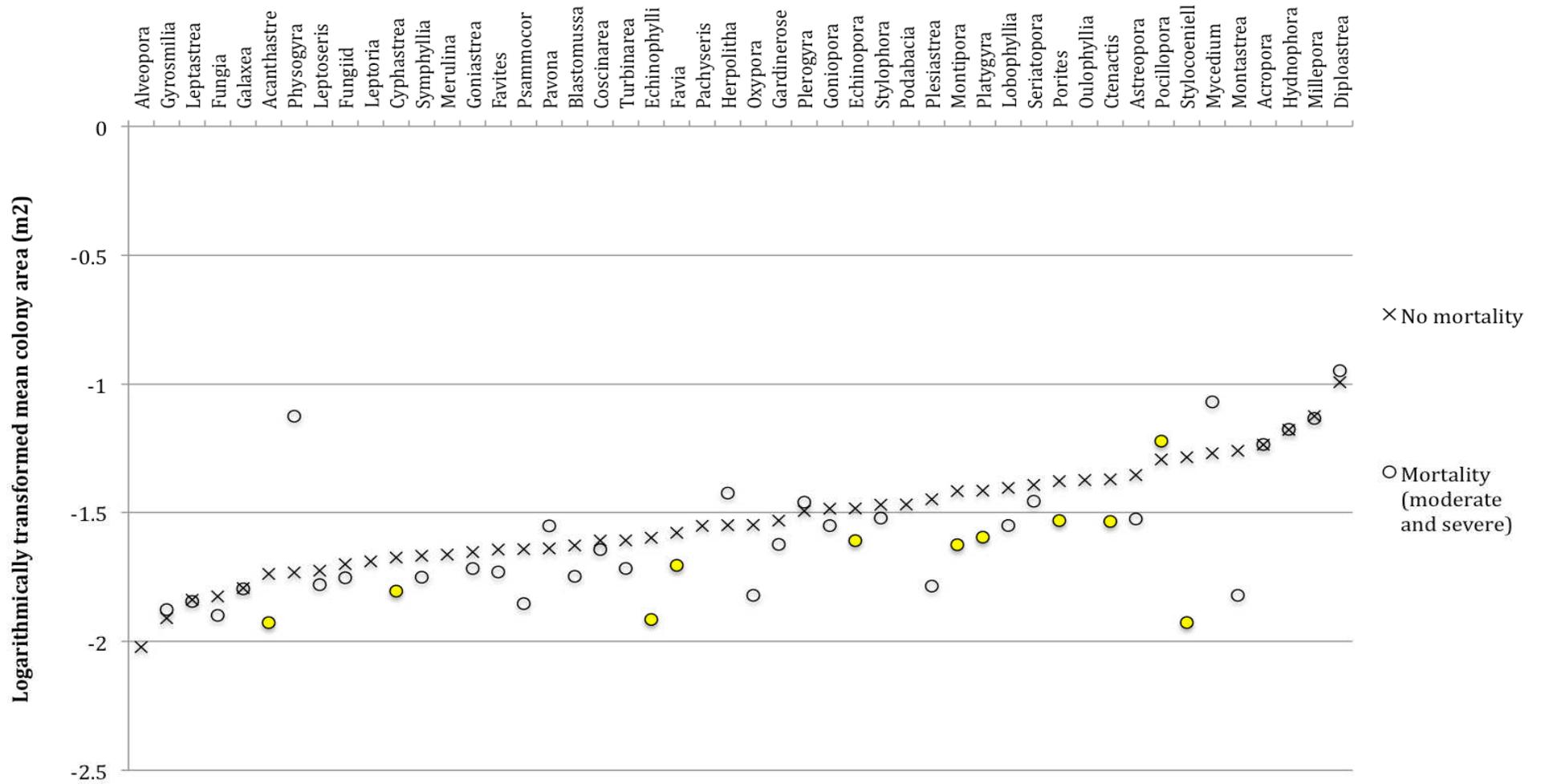


Figure 36. Mean colony size (log area) for all generic populations within the Farasan Banks, Saudi Arabia, with populations subdivided by presence or absence of observed mortality (categories 'moderate' and 'severe' combined). Highlighted data points indicated significantly different population means (two-sample T-test $p \leq 0.05$). Genera ranked by increasing size

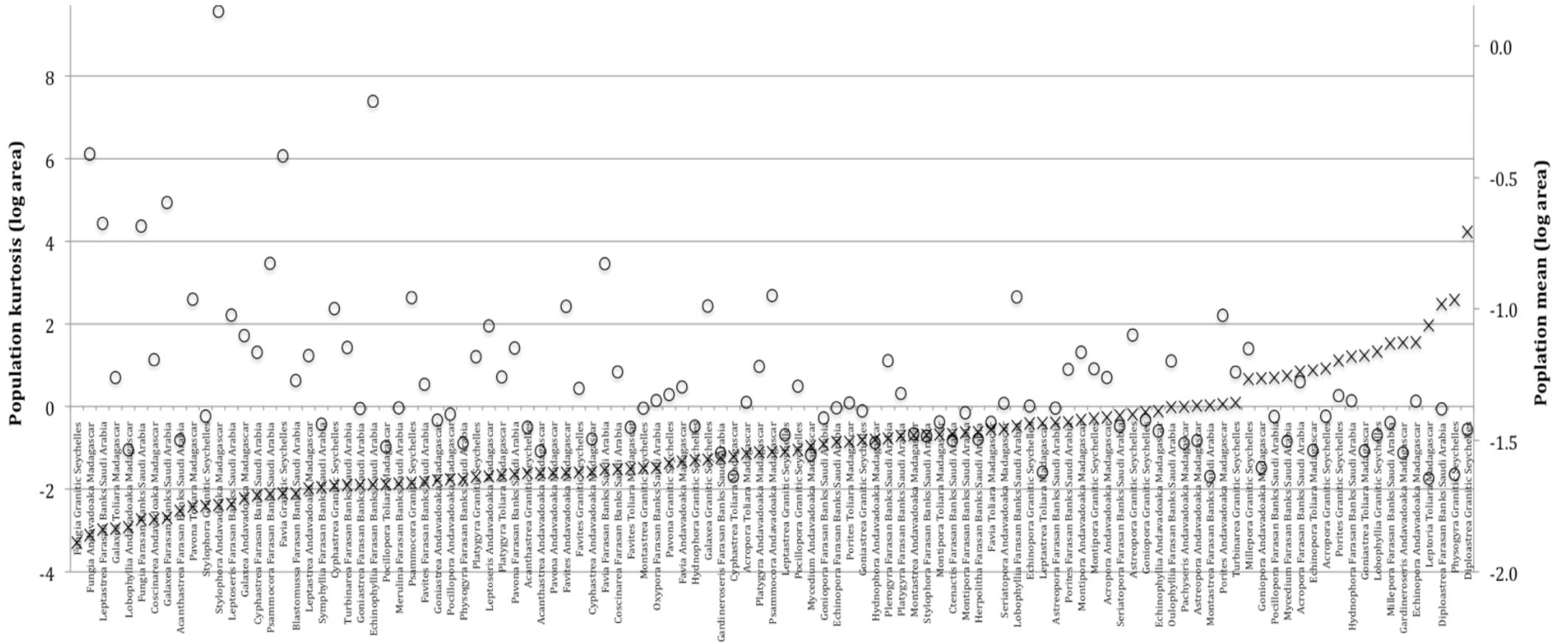


Figure 37(a). Relationships between mean region-specific genus population size (log area) and kurtosis ($r = -0.34$, $p < 0.001$: below), based on all populations consisting of 10 or more colonies. Populations ranked by increasing size

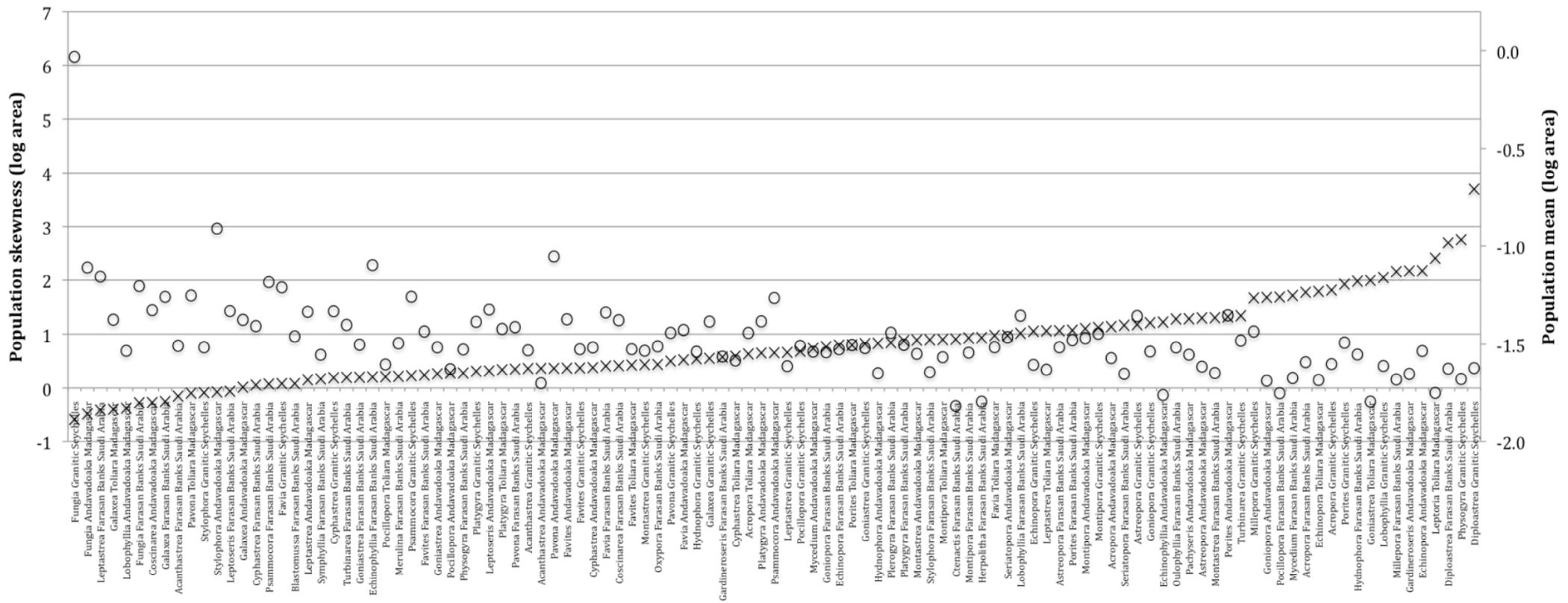


Figure 37(b). Relationships between mean region-specific genus population size (log area) and skewness ($r = -0.55$, $p < 0.001$), based on all populations consisting of 10 or more colonies. Populations ranked by increasing size

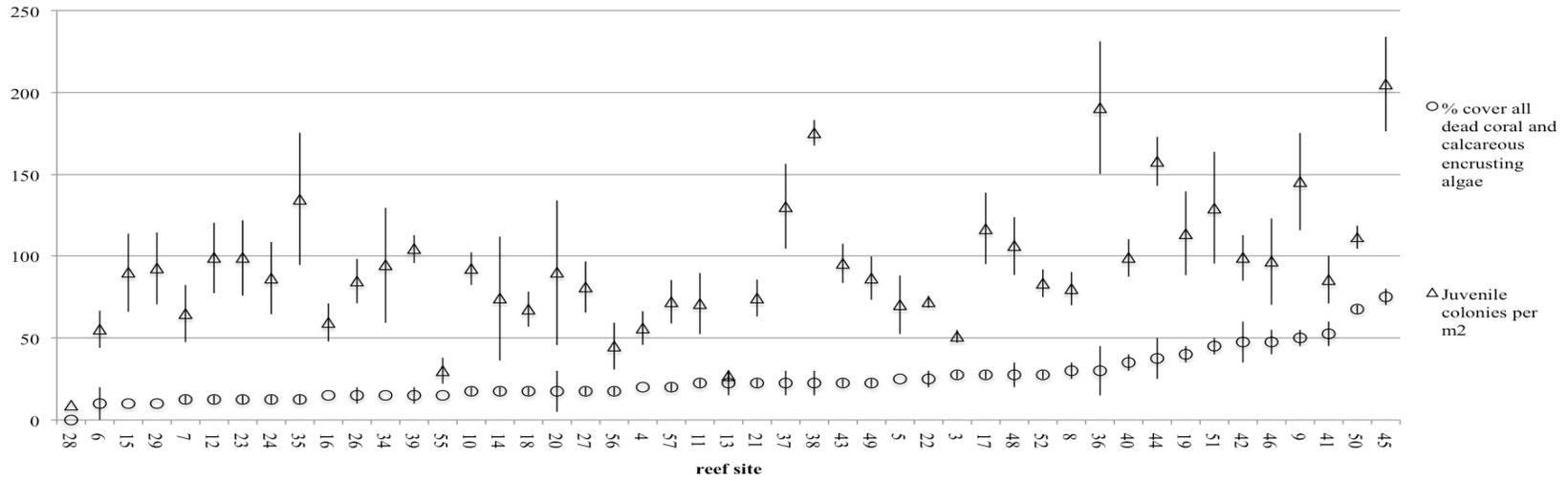


Figure 38. Relationship between juvenile colony density (all taxa) and % cover of hard 'settlement' benthic groups (Pearson $r = 0.31$, $p = 0.037$) (\pm standard error of mean), all Farasan Banks reef sites, ranked by increasing % cover

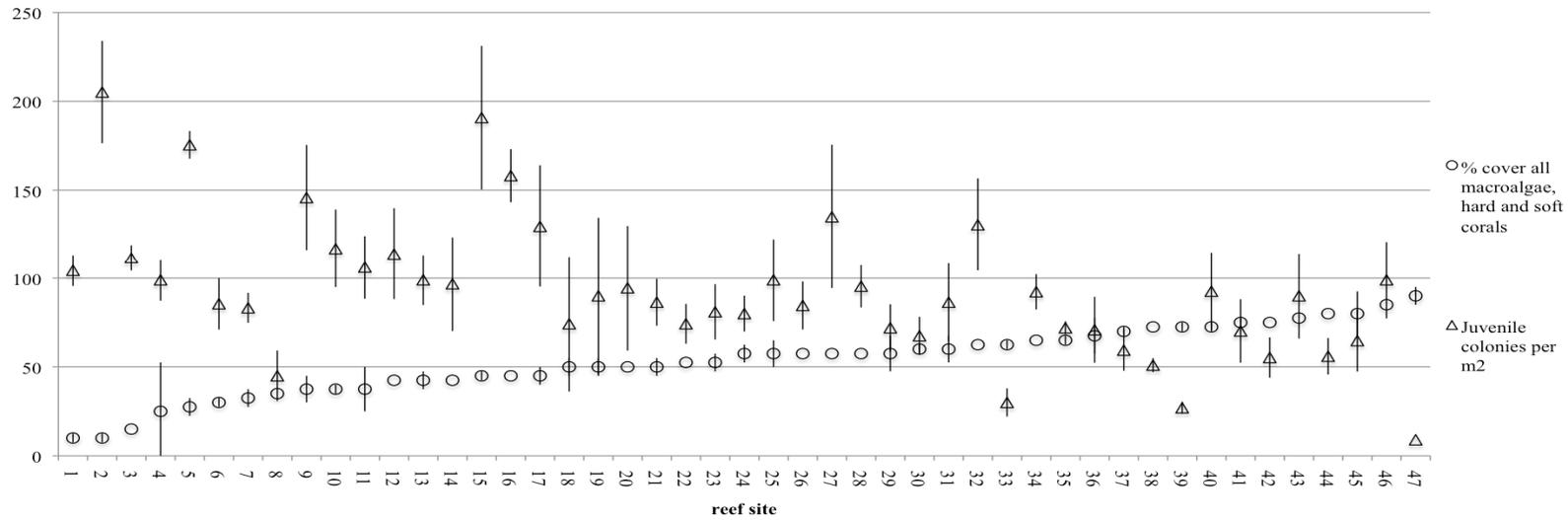


Figure 39. Relationship between juvenile colony density (colonies m^{-2} , all taxa) and % cover of 'non-settlement' benthic groups (Pearson $r = -0.37$, $p = 0.014$) (\pm standard error of mean), all Farasan Banks reef sites, ranked by increasing % cover

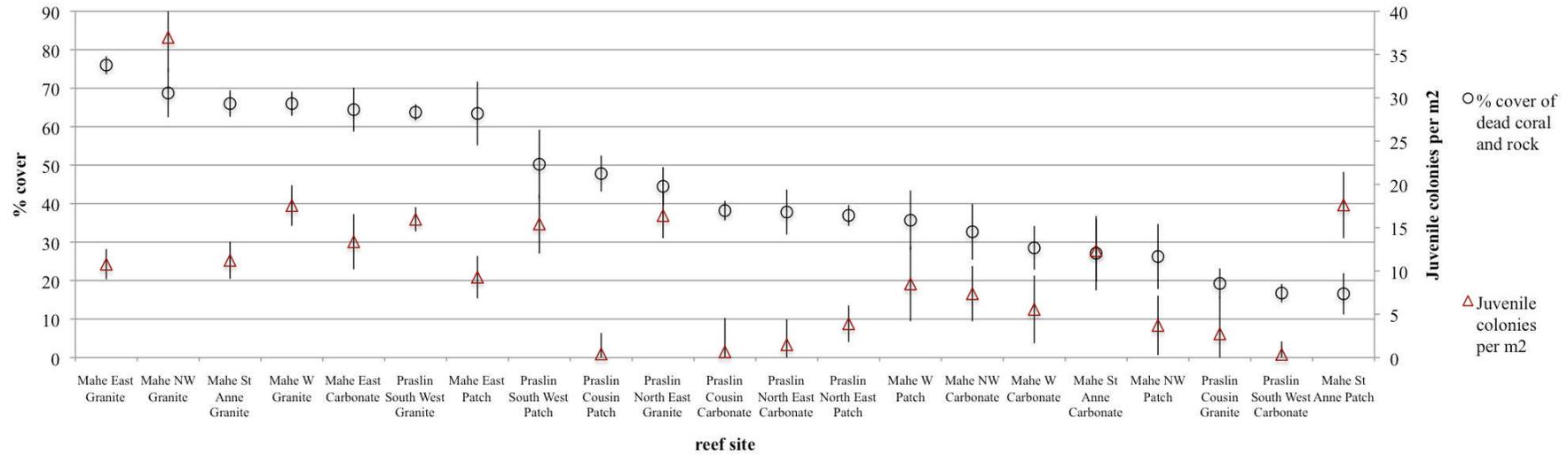


Figure 40. Relationship between juvenile colony density (colonies m⁻², all taxa) and hard 'settlement' benthic groups (Pearson r = 0.50, p = 0.02) (± standard error of mean), all Granitic Seychelles reef sites, ranked by increasing % cover

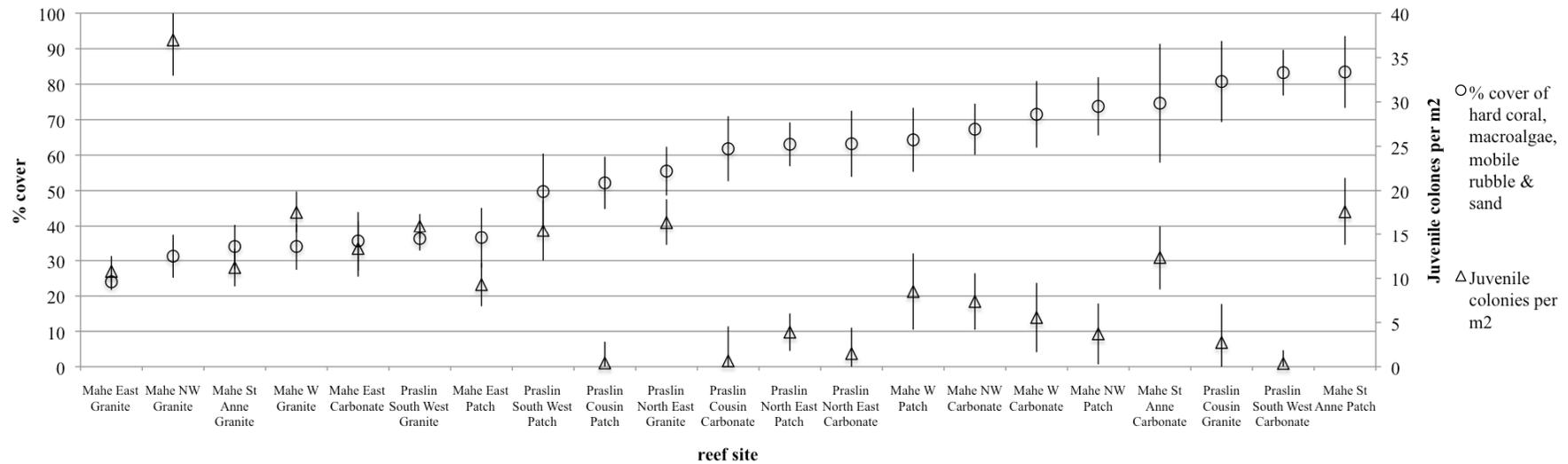


Figure 41. Relationship between juvenile colony density (all taxa) and 'non-settlement' benthic groups (Pearson r = -0.50, p = 0.02) (± standard error of mean), all Granitic Seychelles reef sites, ranked by increasing % cover

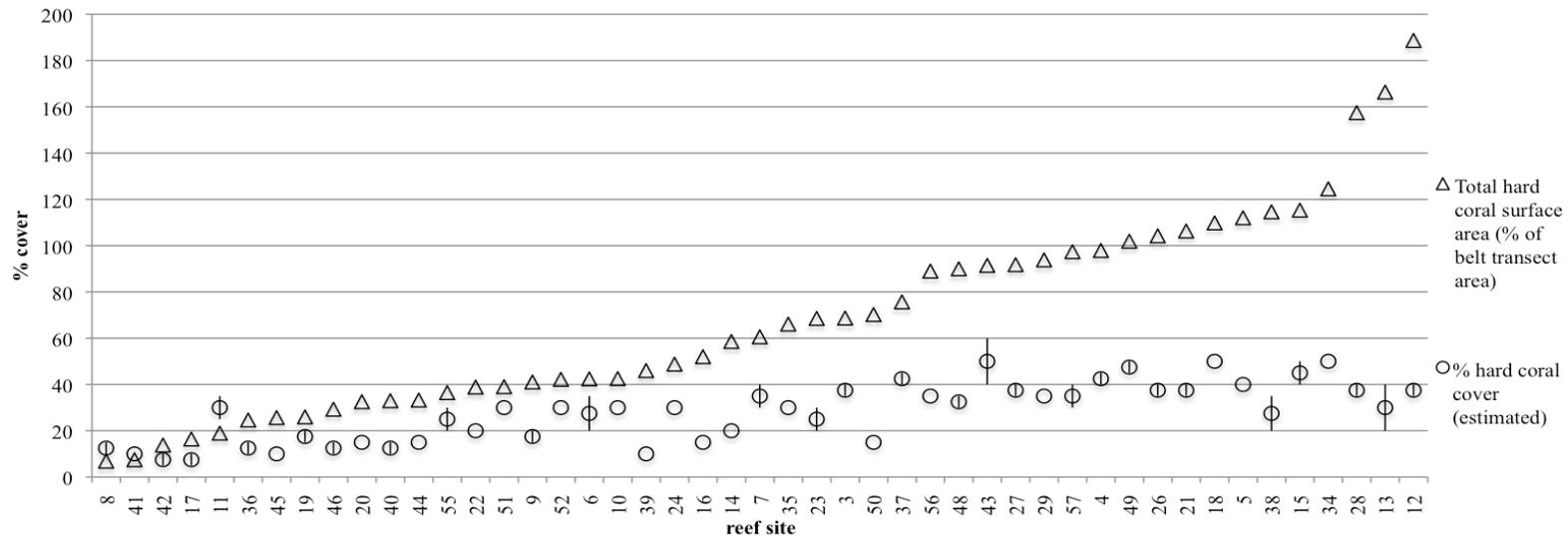


Figure 42. Comparison of mean hard coral cover estimates (\pm standard error of mean) with total hard coral colony surface area measurements, per unit area, Farasan Banks, Saudi Arabia, sites ranked by increasing % cover

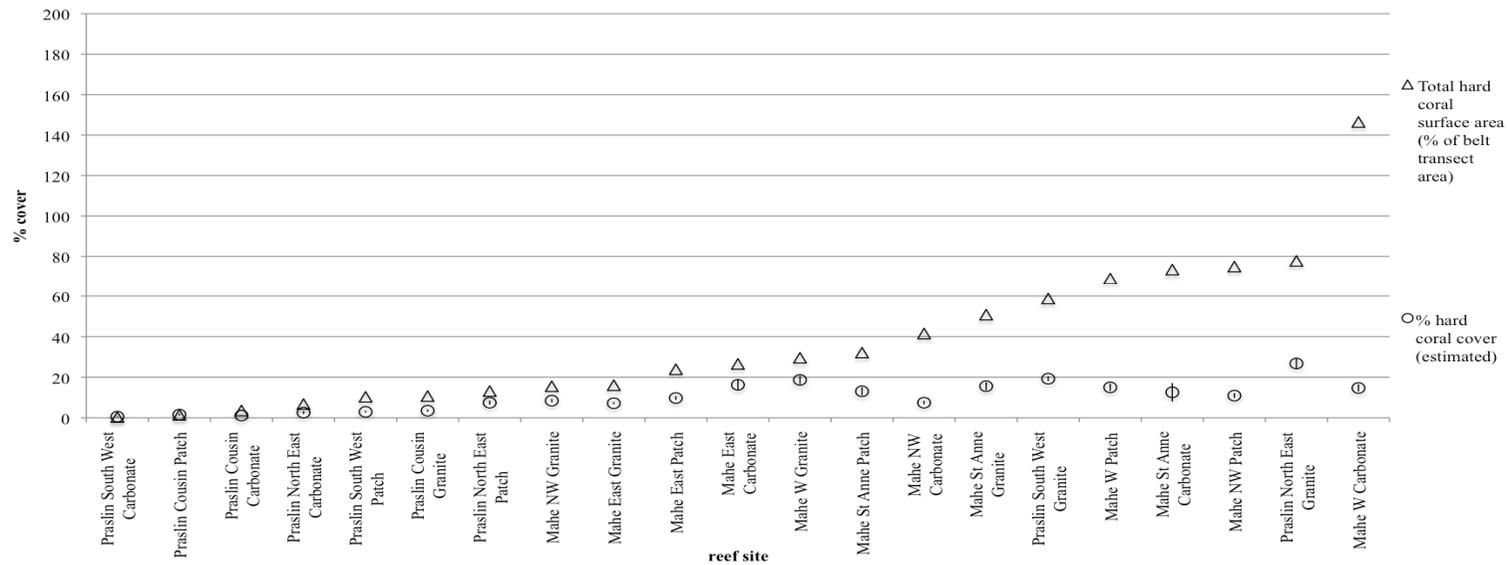


Figure 43. Comparison of mean hard coral cover estimates (\pm standard error of mean) with total hard coral colony surface area measurements, per unit area, Granitic Seychelles, sites ranked by increasing hard coral surface area

7.3 Relationship between juvenile colony density and benthic cover (pooled taxa)

Figure 38 illustrates the relationship between juvenile colony density and percentage cover of hard benthic substrate groups suitable for settlement across all Farasan Banks reef sites (combined cover of calcareous encrusting algae and uncolonised standing dead coral). Pearson correlation analysis shows a weak relationship between the two variables (Pearson $r = 0.31$, $p = 0.037$), indicating that juvenile colony densities are higher where there is a greater availability of unoccupied hard substrate suitable for coral settlement.

There is a stronger negative correlation (Pearson $r = -0.37$, $p = 0.014$) between juvenile colony abundance and cover of live benthic groups unsuitable for recruit settlement (live hard and soft coral, macro and turf algae, sponges and other live benthic groups)(Figure 39). This applied especially to macro-algal cover and juvenile hard colony abundance (Pearson $r = -0.49$, $p = 0.02$). In both cases, values of juvenile colony abundance are those obtained from the use of ultra violet census (see section 2.5.1, page 58). Removal of juvenile colonies identified through UV census from the analyses reduced juvenile abundance values but did not remove the significance of observed correlations.

Notably, there were significantly higher juvenile densities at sites that showed evidence of mass coral mortality than at sites where no mortality was observed (80.2 ± 7.5 SE colonies m^{-2} compared to 59.0 ± 4.8 SE colonies m^{-2} ; two-sample T-test of transformed data $P = 0.02$). These differences were more highly significant when data used included colonies observed with UV census (109.0 ± 9.0 SE colonies m^{-2} compared to 78.3 ± 6.0 SE colonies m^{-2} ; two-sample T-test of transformed data $P = 0.01$).

Stronger correlations between settlement space and juvenile density were recorded in the Granitic Seychelles, despite the far lower values of juvenile coral abundance observed in this more depauperate region (Figure 40 and Figure 41), and despite the lack of use of UV in this region.

Additional negative correlations were again found between juvenile hard colony density and both hard and soft coral cover (individually) (Pearson $r = -0.36$, $p = 0.01$; and $r = -0.37$, $p = 0.01$ respectively). Correlations are calculated separately from the Farasan Banks surveys in view of the different sampling methods for benthic composition assessment used in the two regions.

These results show that a higher abundance of competing benthic groups reduces the available space for coral recruitment, in turn reducing juvenile colony abundance.

7.4 Relationship between benthic cover and total colony surface area

Comparisons of hard coral cover values with measurements of total hard colony surface area, per unit area, are possible for the Farasan Banks (Figure 42) and the Granitic Seychelles (Figure 43). Values of benthic composition shown are the mean percentage cover per site, \pm SEM, based on visual estimates across all replicates. Values of total hard coral surface area represent the combined mean surface area for adult and juvenile colonies, expressed as a percentage of the 2 dimensional surface area of the total sampled area. For example a mean coral surface area value of 6m^2 per 10m^2 sample area equates to 60% total hard coral surface area. In both cases the contributed values of juvenile colony surface area used shown are from surveying without the use of ultraviolet light (section 4.6).

These figures show clearly that coral cover, as defined in conventional benthic composition surveys, bears little similarity to the overall surface area of coral colonies within a reef, whose combined values are almost invariably far greater than measures of 2-dimensional benthic cover from the same habitat. Of the 21 sites for which comparative benthic composition data are available for the Granitic Seychelles, coral surface area values exceeded coral cover estimates in 17 sites, with coral surface area at one site (Mahe West Carbonate) being almost 10 times higher than hard coral cover as estimated from benthic composition surveys (Figure 43; page 129). Across all sites in the Farasan Banks and Granitic Seychelles total hard coral surface area was, on average $2.4 (\pm 0.2 \text{ SE})$ and $3.3 (\pm 0.5 \text{ SE})$ times higher than estimated hard coral cover respectively.

Further, coral surface area values exceeding 100% of the 2-dimensional sampled area are common. Of the 47 sites for which comparative data from the two variables are available from the Farasan Banks, 11 exceeded 100% and 18 exceeded 80% (Figure 42; page 129), compared to only 1 site of the 21 surveyed in the Granitic Seychelles.

Since coral cover – when exceeding 100% of the 2-dimensional reef area – contributes directly to increased reef rugosity, it is suggested that this difference may be a useful measure of rugosity, an otherwise difficult attribute to measure quantitatively in reefs (Wilson et al. 2007).

7.5 Multivariate analysis of coral communities

This section investigates relationships between different reef sites and replicates, using between-sample and between-region tests. Analyses are based on the size frequency distribution of all colonies, the taxonomic composition of colonies, and the size frequency distributions of all colonies across individual taxa.

Coral communities are compared with overall reef benthic composition, and the relative sensitivity is assessed of different multivariate analytical and transformational approaches in discriminating reef sites based on the composition of coral communities.

7.5.1 Size distribution analysis

Multivariate matrices of colony density and surface area for sites (samples) across 9 CCCR size classes (variables) are examined (see also Figure 3; page 75).

7.5.1.1 Between region differences

Differences in the size structure of coral communities between regions (pooled taxa), based on the CCCR colony size class categories, were strongly significant for juvenile communities (global $R = 0.57$, $p < 0.1\%$), and moderately significant for adult communities (global $R = 0.25$, $p < 0.1\%$) (values based on analysis of colony density data).

Inter-region comparison of pooled adult and juvenile size frequency distribution data (pooled taxa) was only possible for the Farasan Banks and Granitic Seychelles. Between region differences were highly significant (ANOSIM global $R = 0.76$, $p < 0.1\%$, based on colony density data), with almost complete separation of samples between the two regions in 2-dimensional MDS ordinations (Figure 45).

Superimposing individual variables (number of colonies unit area per size class) on the ordination in Figure 45 illustrates the differences in the size frequency distributions of coral communities responsible for the separation of samples between the two regions in the ordination. The Farasan Banks show a much higher abundance of juvenile colonies than the Granitic Seychelles, but as colony sizes increase, the relative abundance of larger colonies in the Granitic Seychelles also grows, with the Seychelles sites ultimately showing higher abundance of upper-mid range size classes than Farasan Banks sites (Figure 45).

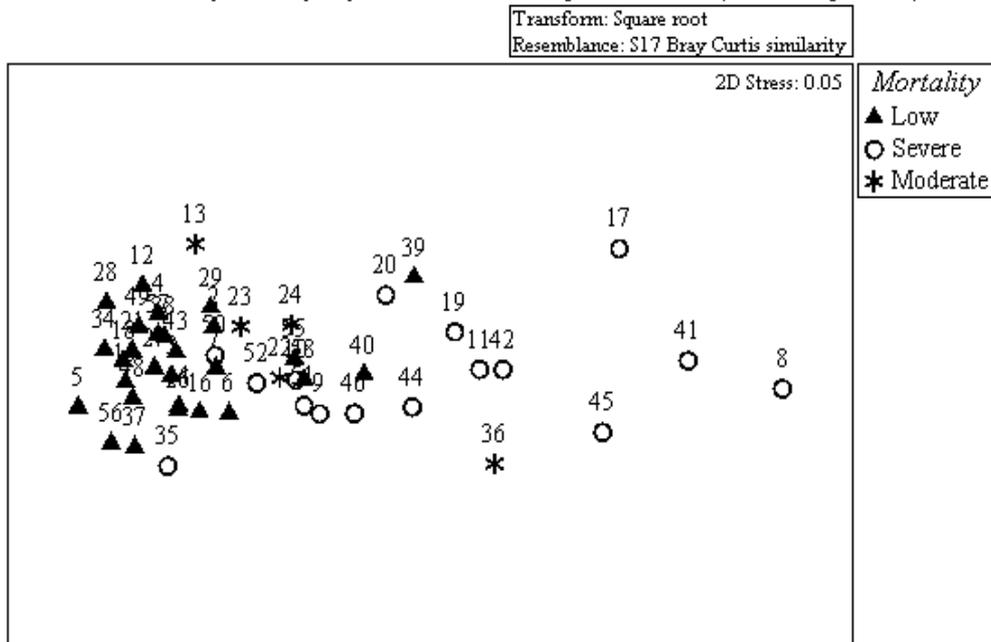
7.5.1.2 Within region analyses

Within the three Farasan Banks groups of sites defined *a priori* by the qualitative factors representing the observed degree of mortality: 'low', 'moderate' and 'severe' (see section 6.3), clear differences were seen in coral community size structure (Figure 44).

Differences were highly significant in the adult coral community (ANOSIM global $R = 0.45$, $p < 0.1\%$), moderately significant across pooled juvenile and adult size classes (global $R = 0.26$, $p < 0.1\%$), but not significant in juvenile size classes alone (global $R = 0.06$, $p = 15.1\%$) (all analyses based on colony density data).

Superimposing individual size class variables on MDS ordinations of samples based on all colony sizes (adult and juvenile combined), shows a distinctly lower abundance of large colonies, as well as a higher abundance of juvenile colonies, at sites affected by severe mortality (Figure 46)

Coral colony density, by adult size class, pooled taxa (colonies per m²)



Coral colony density, by juvenile size class, pooled taxa (colonies per m²)

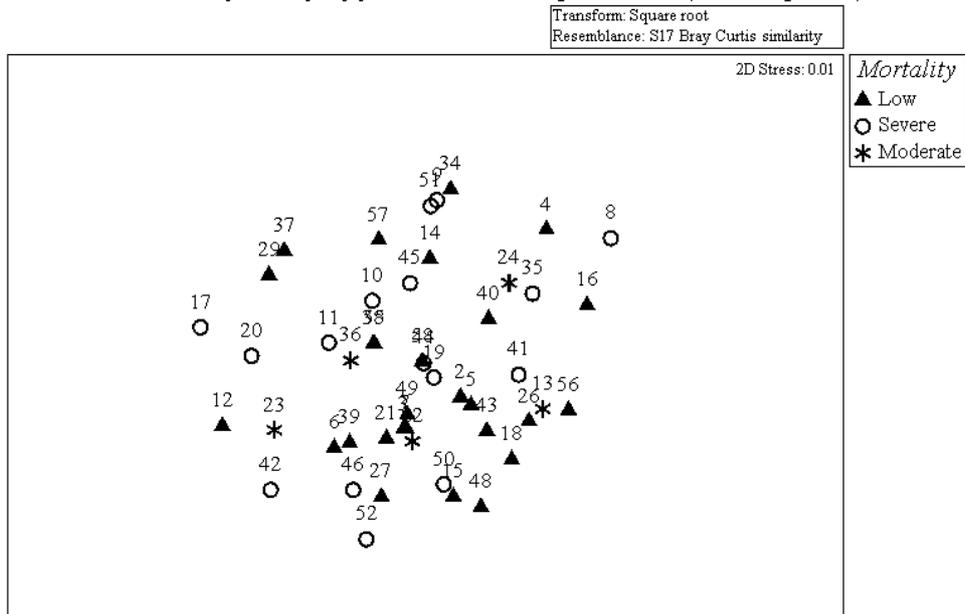


Figure 44. Non-metric MDS ordinations of all samples from Farasan Banks, based on colony density data (pooled taxa), across adult (above) and juvenile (below) all size classes, showing degree of mortality observed. Values for each sample are the mean of all replicates within each site.

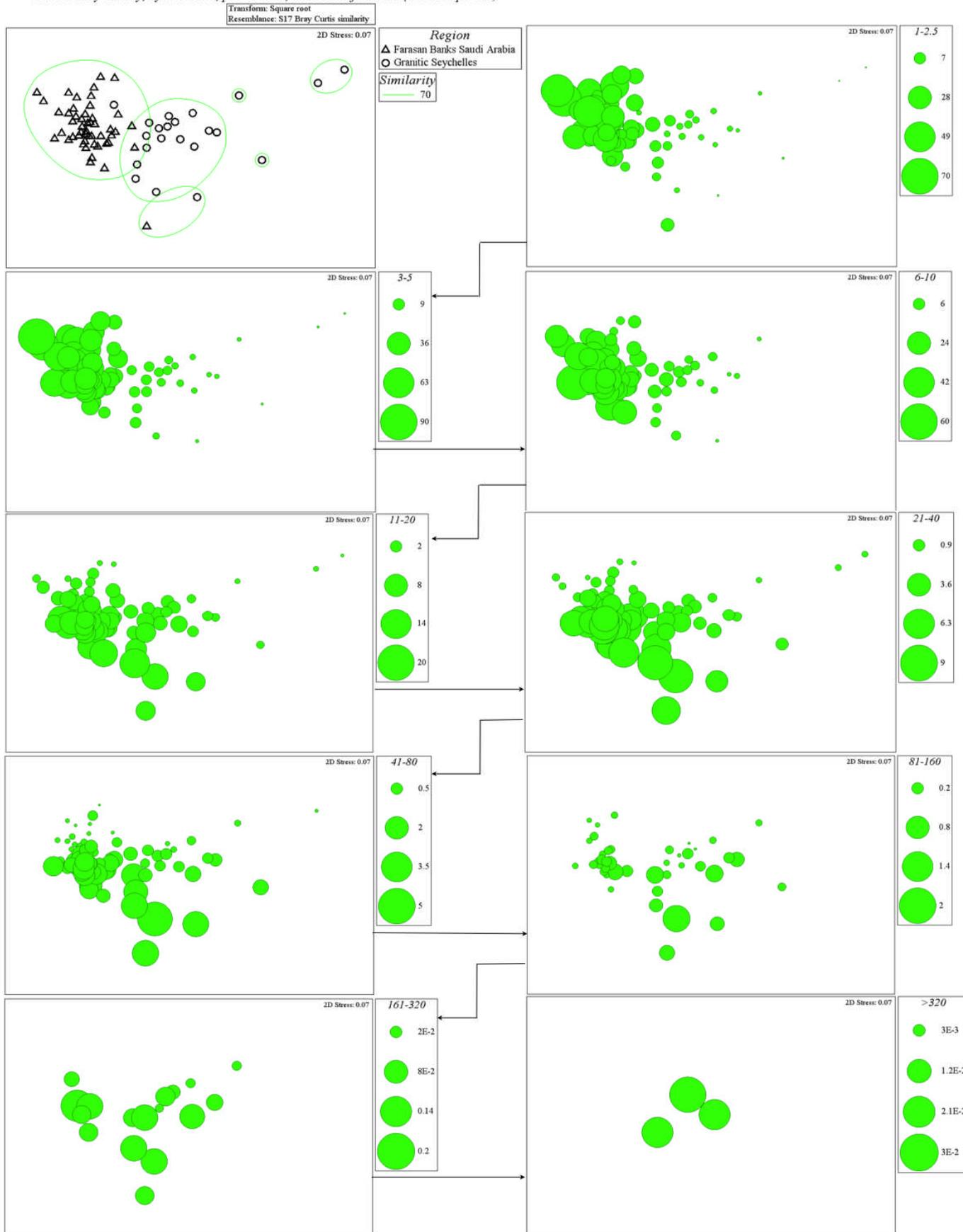


Figure 45. Non-metric MDS ordinations of all samples from Granitic Seychelles and Farasan Banks, based on colony density data (pooled taxa), across all size classes. Values for each sample are the mean of all replicates within each site. Samples grouped within Bray-Curtis similarity boundaries at 70% similarity. Sequential bubble plots show changes in colony density by increasing size class

Coral colony density, by size class, pooled taxa, adults and juveniles (colonies per m2)

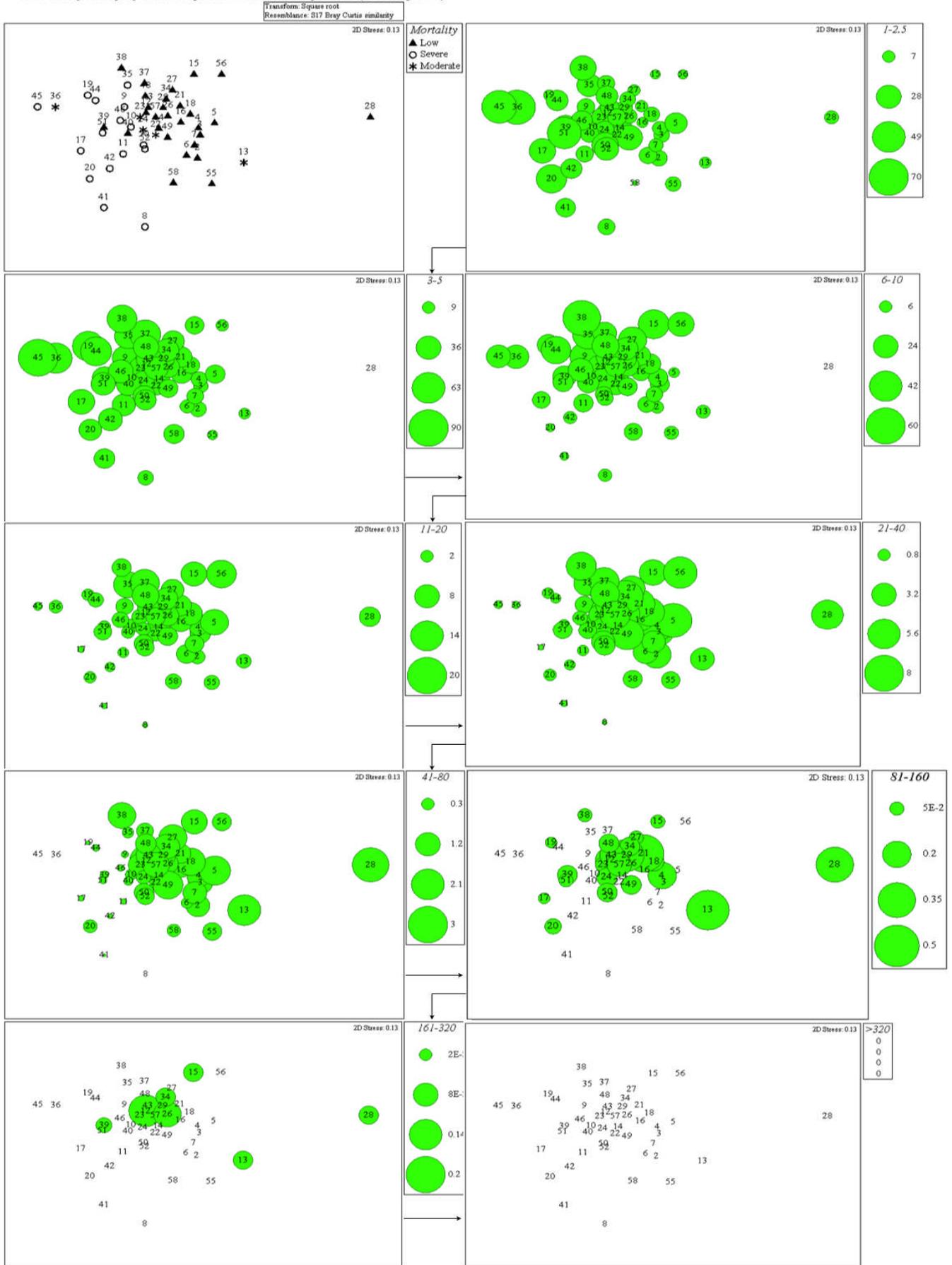


Figure 46. Non-metric MDS ordinations of all samples from Farasan Banks, based on colony density data (pooled taxa), across all size classes. Values for each sample are the mean of all replicates within each site. Sequential bubble plots show changes in colony density by increasing size class.

7.5.2 Taxonomic composition analysis: colony density and surface area by taxa

7.5.2.1 *Between region analyses*

Taxonomic composition of corals varied between sites and regions for both adults and juveniles. MDS ordinations of samples from all regions based on generic and family composition of corals are shown separately for juvenile and adult communities in view of their different sampling approaches (Figure 47 and Figure 48).

These MDS plots illustrate the dissimilarity between sites and regions. The patterns are generally consistent whether based on colony abundance or surface area per taxon.

One-way ANOSIM testing for differences in generic composition of adult corals between regions (all samples; Andavadoaka, Toliara, Farasan Banks and Granitic Seychelles) shows clear differences between the four regions when the analyses are based on colony density (global $R = 0.28$, $p < 0.1\%$) but only weak significance when based on colony surface area (global $R = 0.19$, $p < 0.3\%$). When all sites are pooled there is considerable overlap of samples across regions, as illustrated in Figure 48. Values of Global R calculated across all sites are inevitably depressed on account of the large sample size and considerable within-region heterogeneity in community composition between sites.

Differences in generic composition of juveniles between regions (all samples; Chagos, Farasan Banks and Granitic Seychelles) were much more highly significant, with global $R = 0.61$ ($p < 0.1\%$) for colony density and global $R = 0.52$ ($p < 0.1\%$) for colony surface area. Such large values of R indicate much higher separation of samples by survey region (Figure 47; page 139).

Superimposing univariate genus-specific hard coral density or surface area values on the MDS plots shown in Figure 47 and Figure 48 illustrates changes in the density of individual genera between sites, giving an indication of the role of individual variables in structuring the patterns of dissimilarity seen across the

samples. The resulting 'bubble plots' illustrating changes in colony density and surface area for individual taxa across sites are shown for the adult and juvenile communities (separately) in Appendix 1. In each case plots are shown for the 11 most important genera, in terms of contribution to between-sample dissimilarity, based on results of SIMPER analysis.

These plots highlight striking differences in generic dominance between regions, again emphasising disparities between colony numerical abundance (Figure 85; page 254) and surface area (Figure 86; page 255), as well as dissimilarity between juvenile (Figure 87; page 256 and Figure 88 page 257) and adult communities (Figure 85; page 254 and Figure 86; page 255).

Between-region differences in ANOSIM Global R for adult and juvenile communities cannot be compared directly in most cases, since adult and juvenile data are not both available consistently for all regions (Table 2; page 66). Any direct comparison would thus be specious. A full complement of adult and juvenile coral data is available however for the Granitic Seychelles and Farasan Banks, and repeating the above analysis for these two regions shows highly significant differences between sites for both juveniles and adults. Between region ANOSIM Global R values for juvenile and adult communities, based on colony density data, are 0.813 ($p < 0.1\%$) and 0.446 ($p < 0.1\%$) respectively.

These test results do not imply that coral communities between the two regions have no characteristics in common, but that different characteristic patterns of both adult and juvenile coral community composition are found consistently between the Granitic Seychelles and Farasan Banks.

The MDS plots in Figure 49 illustrate this dissimilarity between coral communities from the two regions, showing also the greater within-region similarity of juvenile and adult coral communities in the Farasan Banks. The Granitic Seychelles shows considerably higher inter-site variability and cluster poorly within the ordination space.

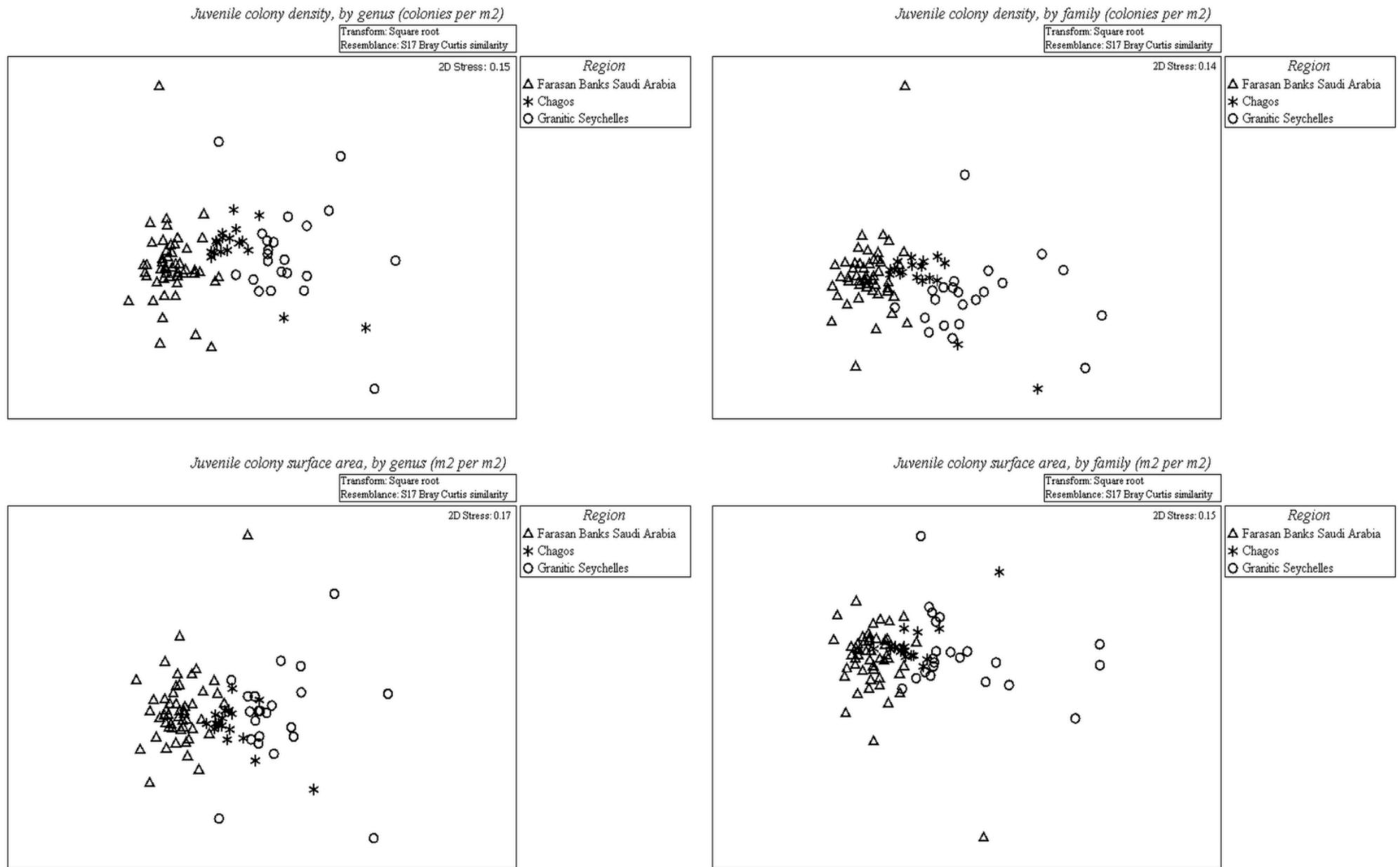


Figure 47. Non-metric MDS ordinations of all samples from all survey regions, based on juvenile colony density and surface area data, across taxonomic variables; genera (left) and families (right). Values for each sample are the mean of all replicates within each site

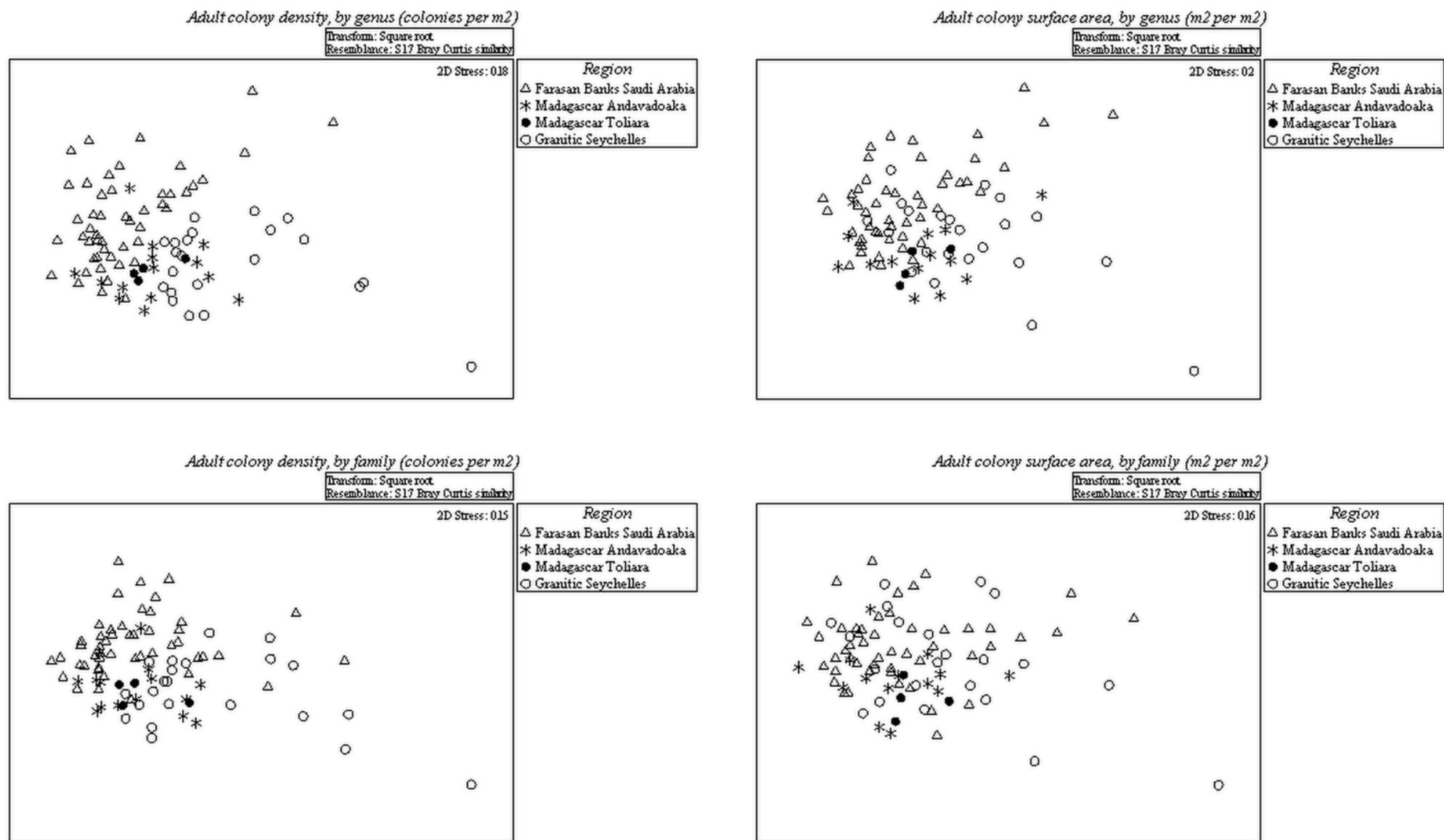


Figure 48. Non-metric MDS ordinations of all samples from all survey regions, based on adult colony density and surface area data, across taxonomic variables; genera (left) and families (right). Values for each sample are the mean of all replicates within each site

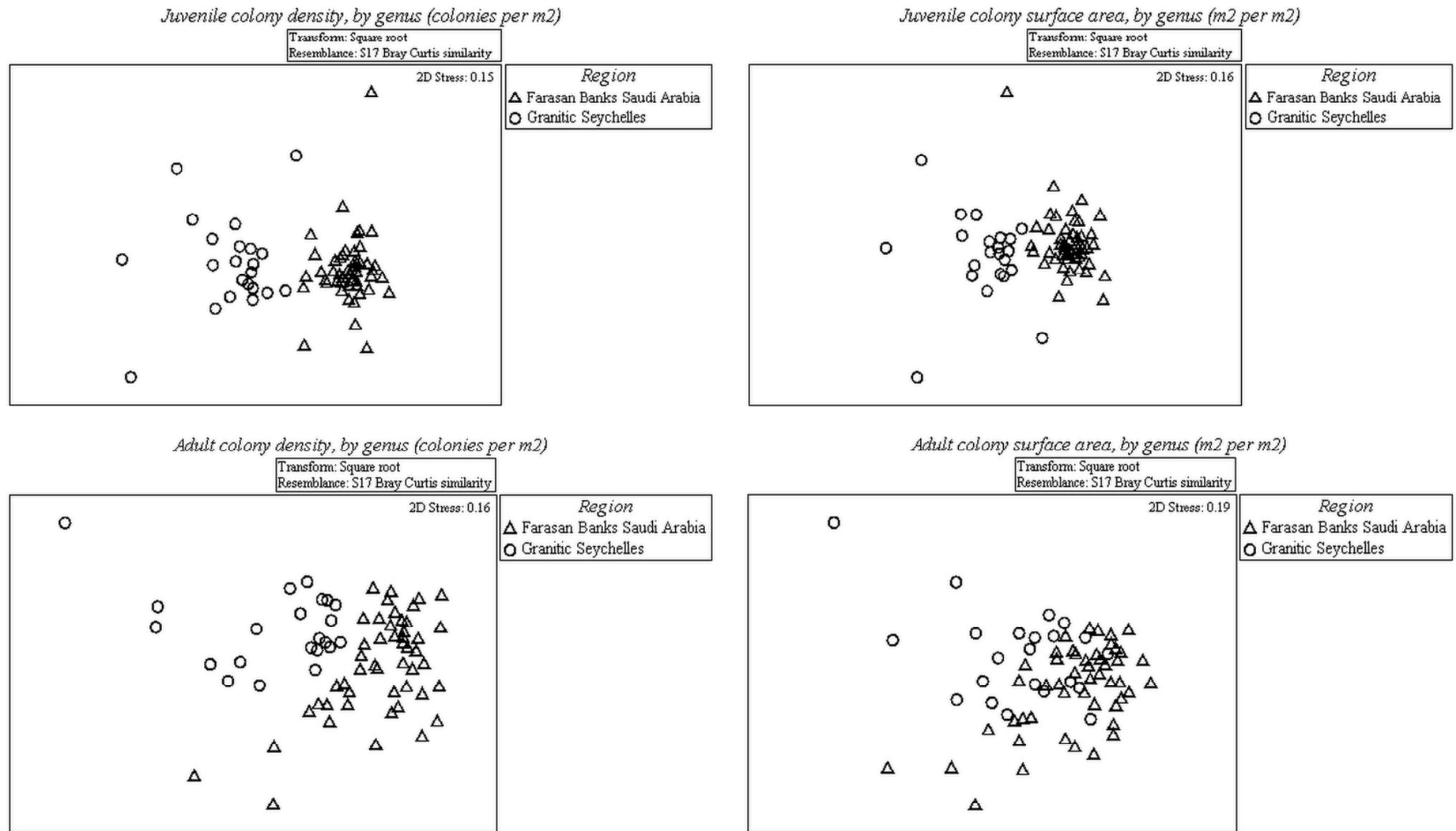


Figure 49. Non-metric MDS ordinations of all samples from Farasan Banks and Granitic Seychelles, based on juvenile (above) and adult (below) colony density (left) and surface area (right) data, across all genera. Values for each sample are the mean of all replicates within each site

7.5.2.2 Within-region analyses

The above routine of discriminating samples using ordination and testing was also carried out to examine the within-region factors that had been identified *a priori*.

In Andavadoaka there is no significant grouping of sites based on the geomorphological reef types categorised by Nadon et al. (2007) (within-region ANOSIM Global R for adult communities based on adult colony density data 0.22 ($p < 0.2\%$)).

In the Granitic Seychelles there is no grouping of sites within the geomorphological substrate classes categorised by Jennings (1996) (within-region ANOSIM Global R values for juvenile or adult communities based on colony density values by genera 0.176 ($p < 0.2\%$) and 0.091 ($p = 8.2\%$) respectively). Indeed, pairwise tests of the 'carbonate' and 'patch' reef categories show negative values of R for both juvenile and adult communities, indicating no evidence of separation of sites within these two factors. There is also no difference between coral communities at protected versus unprotected sites from this region, for either adult or juvenile coral communities (within-region ANOSIM Global R values based on colony density values by genera 0.15 ($p = 10.4\%$) and 0.10 ($p = 21\%$)).

However, there is a visible separation of sites from the Granitic Seychelles island of Mahe from all but two of the sites at Praslin Island (Figure 50). This grouping of sites by the two islands is highly significant; between-island Global R for juvenile and adult communities based on colony density data 0.29 ($p < 0.1\%$) and 0.46 ($p < 0.1\%$) respectively.

The bubble plots in Figure 51 show the differences in density of *Porites* and *Acropora* colonies between sites from the two islands, for both adult and juvenile communities, emphasising the extremely depauperate nature of Praslin reefs.

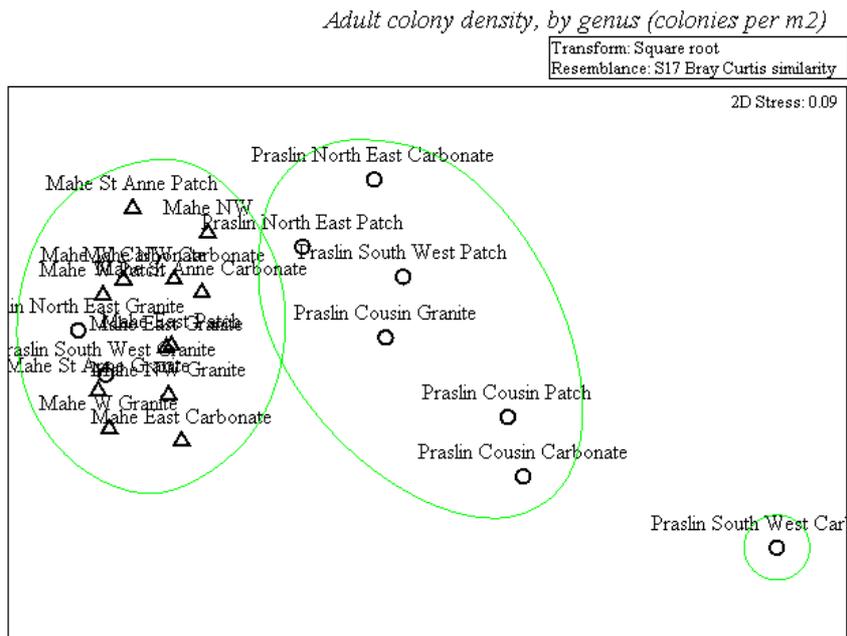
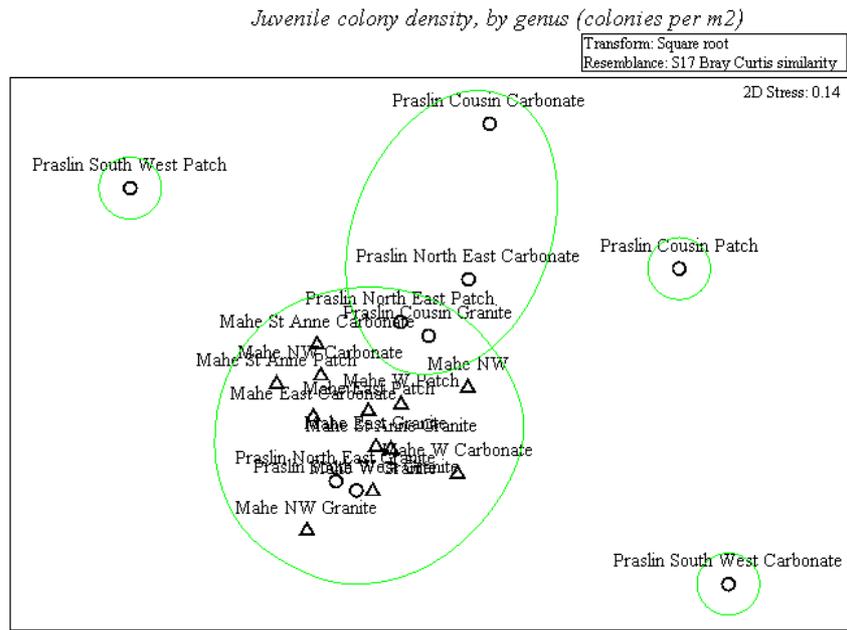


Figure 50. Non-metric MDS ordinations of all samples from Granitic Seychelles, based on juvenile (left) and adult (right) colony density data, across all genera. Circles indicate values from Praslin Island, triangles from Mahe Island. Values for each sample are the mean of all replicates within each site. Samples grouped within Bray-Curtis similarity boundaries at 40% similarity



Figure 51. Bubble plots showing variations in density of *Acropora* and *Porites* colonies across samples based on MDS ordination in Figure 50

Within the Farasan Banks, clear differences were seen between sites based on the degree of mortality observed ('low', 'moderate' and 'severe')(section 6.3; page 86). These samples showed significant separation when variables were abundance values for individual adult coral genera (ANOSIM Global R = 0.34, p = 0.1%). No separation was seen when the analysis was repeated using juvenile colony abundance data (Global R = 0.00, p = 62%), indicating that juvenile colony composition did not change where mortality had been observed (Figure 52).

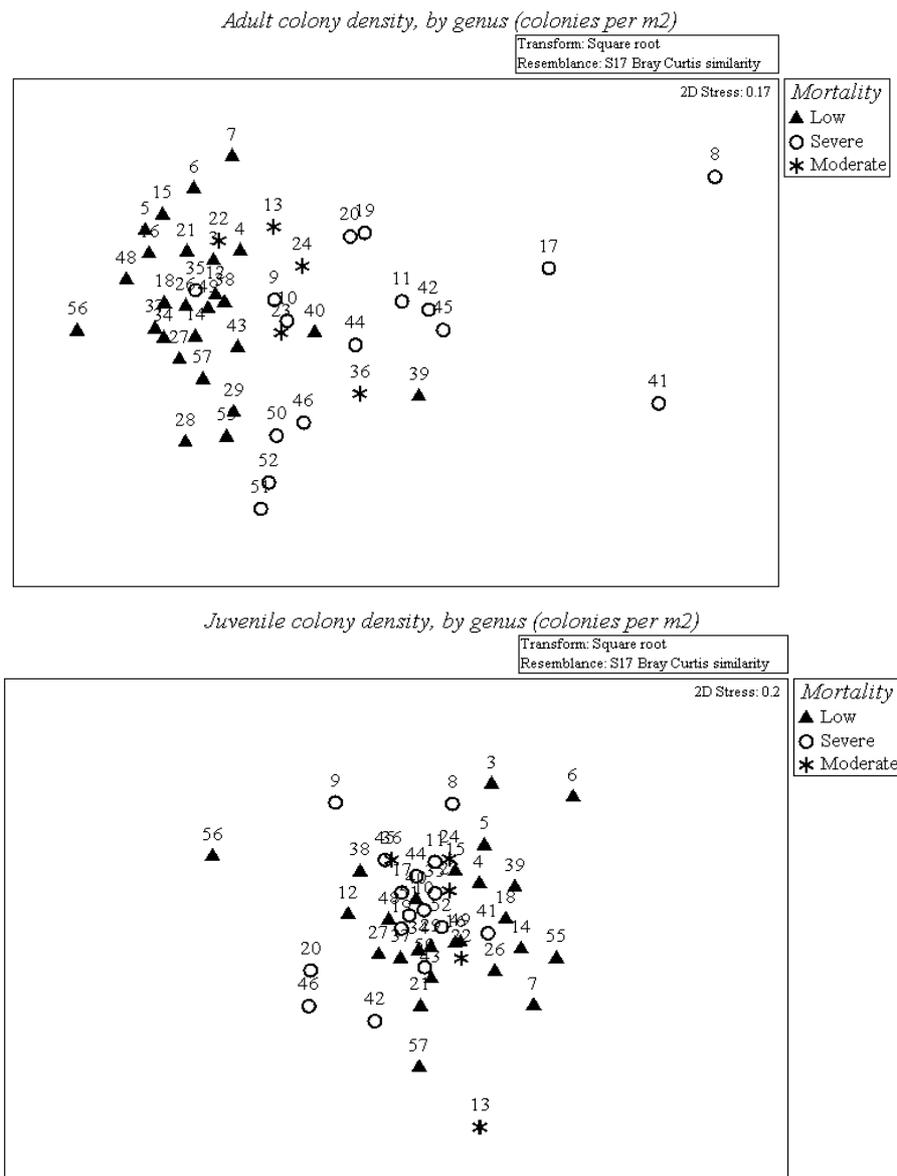


Figure 52. Non-metric MDS ordinations of all samples from Farasan Banks, based on adult (left) and juvenile (right) colony density data, across all genera, showing degree of mortality observed. Values for each sample are the mean of all replicates within each site

7.5.2.3 Effect of depth (juvenile colonies only)

While most surveys were carried out at consistent depths, in Chagos depth separations were possible. Analysis of Chagos juvenile hard coral diversity (colonies $\text{genus}^{-1} \text{m}^{-2}$) by depth showed significant differences between depths (2-way ANOSIM $R = 0.75$, $p < 0.05$), but no differentiation between atolls ($Rho = 0.122$, $p < 0.3$) (Figure 53).

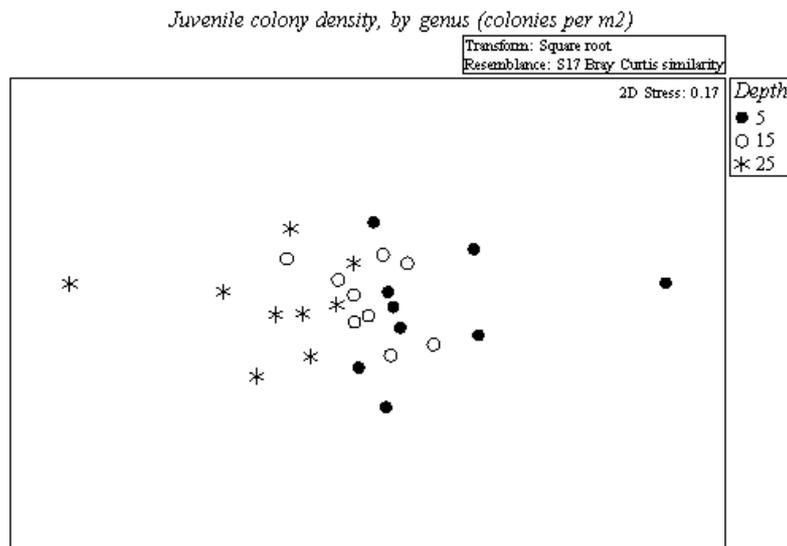


Figure 53. Non-metric MDS ordinations of all samples from Chagos based on juvenile colony density data, across all genera, showing effect of depth on sample similarity. Values for each sample are the mean of all replicate quadrats within each site

SIMPER analysis of variations in the density of recruits from individual genera (across all of the samples involved in the analysis) illustrates depth preferences of dominant genera, which showed the following patterns (Harris and Sheppard 2008):

- Those favouring shallow depths (5m)– *Acropora*, *Porites*, *Acanthastrea* and *Hydnophora*;
- Those favouring medium depths (15m)– *Galaxea*, *Physogyra*, *Oxypora*, *Platygyra* and *Mycedium*;
- Those favouring deep depths (25m) – *Pachyseris*, *Podabacia*, *Seriatopora*, *Leptoseris*, *Gardineroceris* and *Stylocoeniella*;
- No clear depth preference – *Pavona*, *Favia*, *Favites*, *Psammocora*, *Fungia*, *Montipora*, *Pocillopora*, *Goniastrea*, *Leptastrea* and *Lobophyllia*.

7.5.2.4 Effect of sampling effort

Within-region inter-sample dissimilarity is much greater in the Granitic Seychelles than other regions for both the juvenile and adult communities, as well as in Chagos for juvenile communities. This can be seen by the relatively greater spread of samples in ordination space (Figure 54). In both these regions, sampling effort was much higher than at other regions (Table 8). The relationship between sampling effort (number of replicate transects or quadrats per reef site) and between-site dissimilarity is shown in Figure 54.

Table 8. Range and median numbers of replicate samples gathered by region for juvenile and adult coral communities

Survey region	Range of juvenile quadrats per site (median)	Number of adult transects per site (median)
<i>Chagos</i>	31-71 (46)	NA
<i>Granitic Seychelles</i>	28-170 (90)	8-15 (10)
<i>Saudi Arabia Farasan Banks</i>	2-10 (5)	1-6 (2)
<i>Madagascar Andavadoaka</i>	NA	1-8 (2)
<i>Madagascar Toliara</i>	NA	2 (2)

Bray-Curtis coefficients are greatly affected by presence/absence values of variables (in this case taxa) as well as the quantitative values of individual variables. The main impact of increasing the number of replicates making up each sample on the resulting Bray-Curtis dissimilarities between samples is an increase in the number of taxa recorded within each sample (a result of genus accumulation, as shown in (Figure 61; page 160).

However, these patterns do not necessarily imply causation of the observed differences in community structure as a result of the increasing sampling effort at Seychelles sites (median 10 replicate transects per site compared to median 2 replicates at all other regions, Table 8). This is because, where sampling effort differed between sites, this generally changed for all sites within regions, with surveying effort being dependent on logistical parameters within each region. The observed patterns could thus equally be a result of true ecological differences between regions rather than sampling effort.

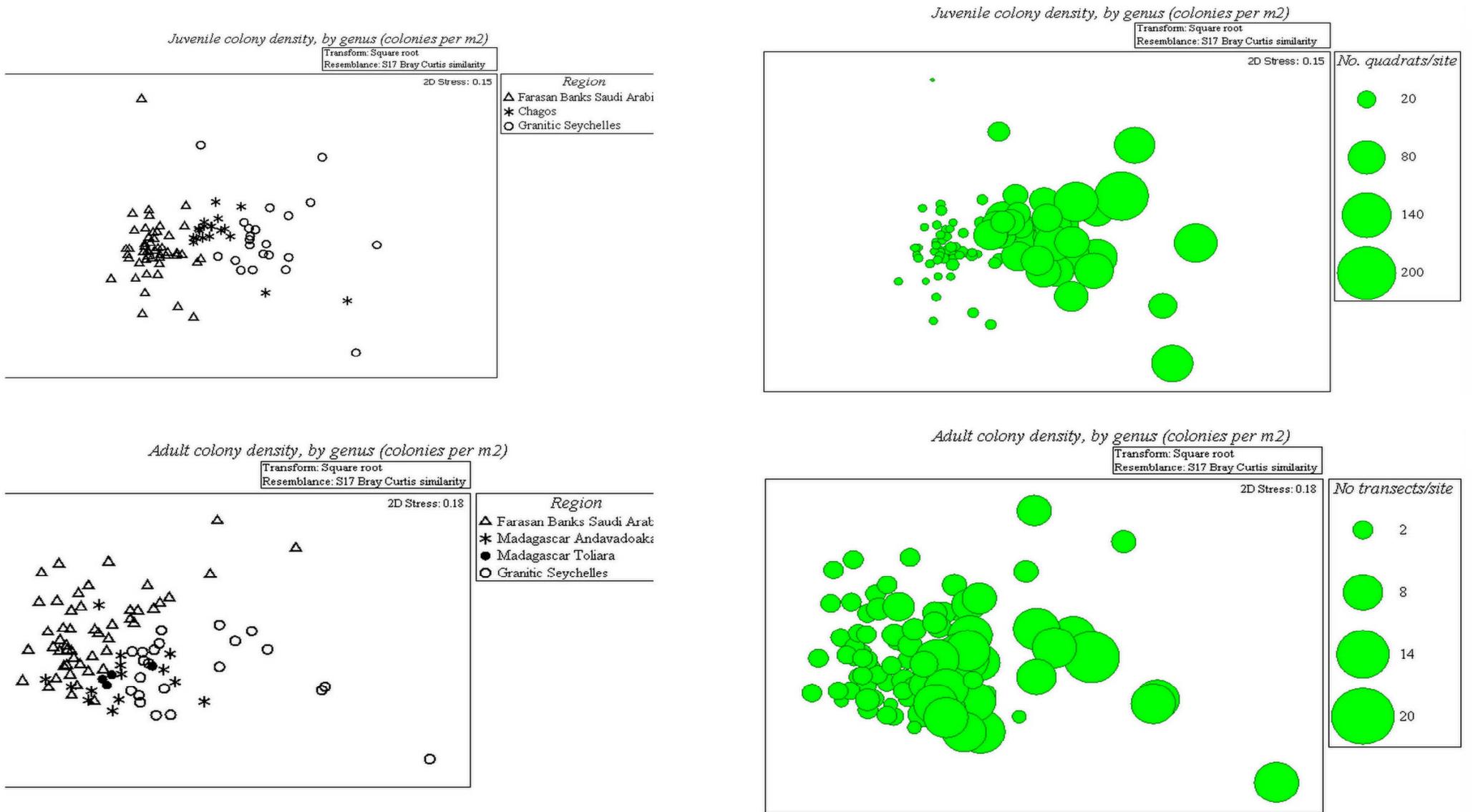


Figure 54. Numbers of replicate quadrats and transects making up each sample (reef site) for juvenile and adult communities respectively, superimposed on colony density (by genus) MDS ordinations

To assess the possible impact of between-region differences in sampling effort (replicate adult transect numbers per site), analysis of all sample-by-taxa matrices was repeated without transforming the raw data for each variable, as a means of placing greater emphasis on commoner taxa making up more of the area cover, and down-weighting the relative importance of presence/absence values for individual taxa. The resulting ANOSIM test results (Table 9) add strength to the conclusion that the between-region differences are not an artefact of differential sampling effort, since values of either R or the significance of R increased in all of four cases when the raw data were analysed without transformation.

Table 9. ANOSIM test results for adult and juvenile coral taxonomic composition, based on both colony density and surface area data, showing impact of $\sqrt{}$ transformation on values of Global R

Survey cohort	Colony density Global R ($\sqrt{}$ transformation)	Colony density Global R (no transformation)	Colony surface area Global R ($\sqrt{}$ transformation)	Colony surface area Global R (no transformation)
<i>Adult corals (all taxa)</i>	0.276 (p<0.1%)	0.344 (p<0.1%)	0.187 (p<0.3%)	0.148 (p<0.2%)
<i>Juvenile corals (all taxa)</i>	0.614 (p<0.1%)	0.674 (p<0.1%)	0.517 (p<0.1%)	0.573 (p<0.1%)

This interpretation is further supported by repetition of the MDS ordinations and ANOSIM testing based on the individual replicates making up all samples across all regions (rather than basing analyses on site values calculated as mean average values of all within-site replicates).

The resulting ordinations (Figure 55 for adult colonies) maintain the separation (and higher spread) of the Seychelles sites away from other regions, with a Global R significantly different to zero (0.14, $p < 0.1\%$). Again, this depressed Global R is legitimately interpretable as highly significant (pers. comm. Clarke, R., 2010), given the very large sample size and spread of samples (403 replicates in this case).

Thus differences in between-region coral community composition are conclusively attributable to real differences in community structure between regions, rather than being an artefact of sampling effort.

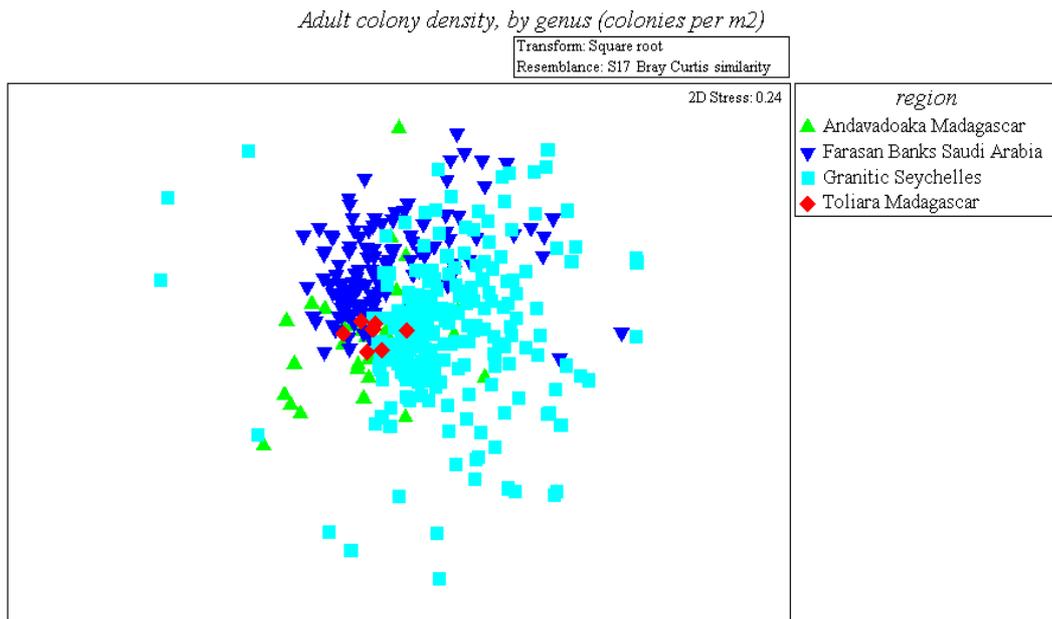


Figure 55. Non-metric MDS ordinations of all replicates from all sites within all regions based on adult colony density data, across all genera

7.5.3 Taxonomic analysis (all regions, subdivided by CCCR size class)

This analysis is based on multivariate matrices composed of values of colony density and surface area for sites (samples) by all CCCR size classes for all genera (variables)(see also Figure 3; page 75).

Significant differences in coral communities were identified between regions based on all size classes of all taxa combined. Levels of significance were similar to those obtained for earlier analysis of both community taxonomic composition and size class variables (individually; sections 7.5.1 and 7.5.2 respectively), and again found juvenile sites being more highly separated by region than adult sites (global $R = 0.55$ and 0.33 respectively, $p < 0.1\%$, when based on colony density data). For the Granitic Seychelles and Farasan Banks, where pooling of juvenile and adult colony data was possible, differences between the Granitic Seychelles and Farasan Banks were very strongly significant (global $R = 0.79$, $p < 0.1\%$), when based on colony density data.

These results further strengthen conclusions that clear differences in both community composition and size frequency distribution of coral communities occur between regions.

7.5.4 Matching and comparison of multivariate patterns

The results of 2nd stage analyses to illustrate the relatedness of the outcomes of the different multivariate analyses are shown in Figure 56.

Different levels of transformation alter the way in which different samples representing coral assemblages are structured in ordinations; the more abundant taxa play a progressively smaller role in influencing between-sample variation as transformation becomes increasingly severe ($\sqrt{}$, $\sqrt{\sqrt{}}$, log). Results of the different analysis options show far less agreement (lower clustering) with increasing severity of transformation, most notably when raw data are based on presence/absence values alone. However these changing patterns of distribution based on changing transformations are not significant (ANOSIM $R = 0.09$, $p < 0.1\%$)(Figure 56).

Similarities between analyses based on adult and juvenile data (separately) show a predictable trend of grouping of analyses in the two cohorts, with a separate intermediate grouping of analyses based on the results of pooled adult and juvenile data ($R = 0.52$, $p < 0.1\%$)(Figure 56).

Changing the analysis variable from genus to family has little impact on the outcome, whereas substituting coral taxon for colony size class results in very different groupings. Amalgamation of colony size class within colony taxon results in outcomes approximately between the two ($R = 0.23$, $p < 0.1\%$)(Figure 56).

Changing the data units from colony density to total colony surface area does not change the results significantly ($R = 0.04$, $p < 3\%$), but does increase the dissimilarity between analysis outcomes, with colony density leading to far higher clustering. This is likely to be due to the far higher variation between samples and variables in colony surface area values than colony density values, which remained untransformed during multivariate analysis.

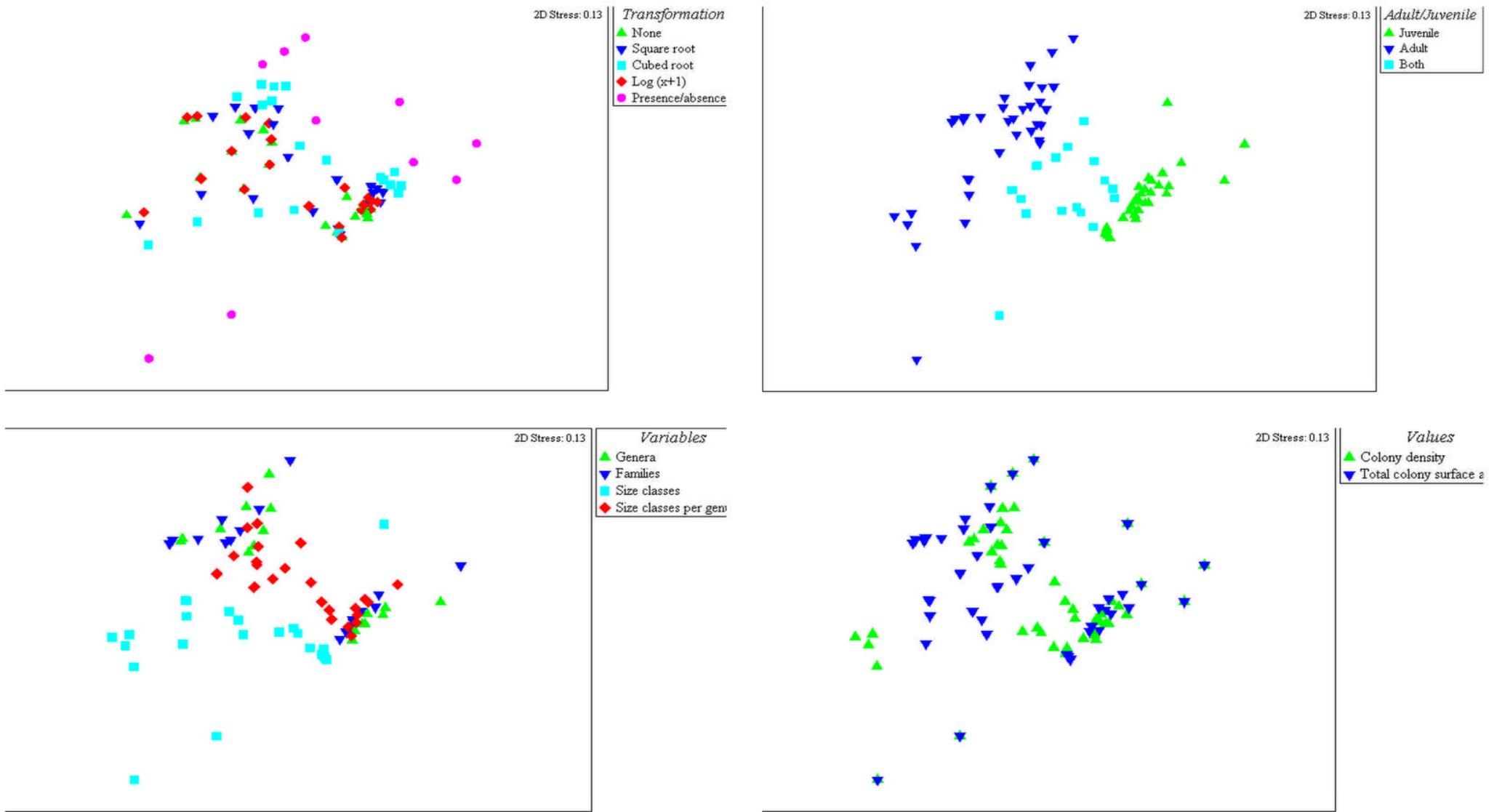


Figure 56. 2nd stage MDS ordination of relatedness of different multivariate analysis outcomes, showing impact of different transformations (top left), variables (bottom left), cohorts (top right) and values (bottom right)

7.5.1 Comparison of coral community data against coral cover data

Resemblance matrices based on different growth form categories of 'coral cover' derived from benthic composition data from the Granitic Seychelles were closely related to matrices based on coral generic composition (methods section 5.3.6; page 74).

This close similarity was maintained whether benthic composition data were measured values of hard coral cover (LIT) or visual estimates of hard coral growth forms, and whether coral community composition data were based on total colony abundance or surface area values, for either adult or juvenile colonies (see methods section 4.7.1). In all cases similarity to coral community data was lower when based on juveniles than on adults. This is to be expected given the comparatively very low contribution to overall benthic cover made by small juveniles (demonstrated in section 7.1.2; page 96).

Similarity between the different coral cover assessment approaches was much lower when measures of benthic composition comprised estimates of all benthic groups – the close similarity was only maintained when the methodological comparisons were restricted to variables describing the hard coral community. This is again to be expected given the absence of non-coral faunal groups and variables in the data collected in this research.

Spearman correlation coefficients of the relatedness of the different sampling approaches are summarised (Table 10). These values are based on all combinations of pairwise RELATE tests between the different forms of benthic composition data and coral community composition data for the Granitic Seychelles. The matching coefficient ρ indicates the relatedness of two similarity matrices, with a value of zero when there is no similarity whatsoever between the two. Variation in coral cover, derived from LIT measurements, across an ordination of samples based on independently-derived coral generic composition data (from colony density data), illustrates the strong relationship between these two methods of assessing coral reef composition (Figure 57).

Table 10. ρ values from Spearman correlation analysis of relatedness of different multivariate analysis outcomes based on the same samples, from Granitic Seychelles (all data $\sqrt{}$ transformed)

<i>Benthic composition survey</i>	<i>Coral colony generic composition data</i>	
	colony density (per unit area, by taxa)	coral colony surface area (per unit area, by taxa)
line intercept transect (LIT) – all hard coral genera	Adt = 0.71 (0.1%) Juv = 0.66 (0.1%)	Adt = 0.68 (0.1%) Juv = 0.67 (0.1%)
visual estimates of hard coral growth forms only	Adt = 0.77 (0.1%) Juv = 0.59 (0.1%)	Adt = 0.79 (0.1%) Juv = 0.62 (0.1%)
visual estimates of all benthic groups	Adt = 0.47 (0.1%) Juv = 0.33 (0.2%)	Adt = 0.44 (0.1%) Juv = 0.27 (0.1%)

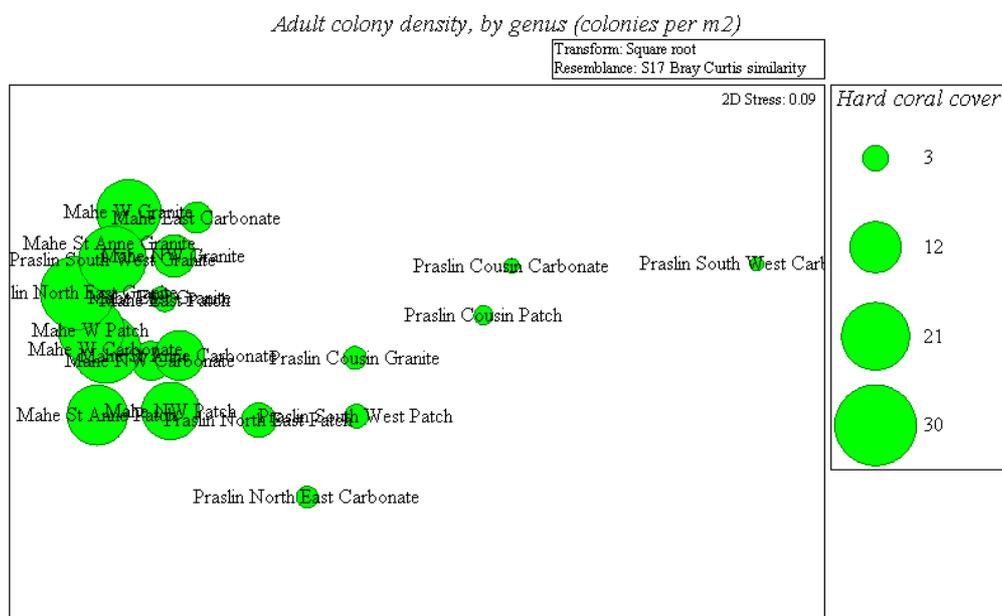


Figure 57. Bubble plot showing variations in total measured hard coral cover across samples from the Granitic Seychelles (from LIT measurements) projected in MDS ordination based on independently derived colony density data, across all genera

Neither methodological approach (benthic composition or coral community composition surveys) enabled discrimination of sites based on the geomorphological factors identified *a priori* (Jennings 1996), with non-significant ANOSIM test values in all cases.

Repetition of the pairwise RELATE analyses (Table 10) for surveys from the Farasan Banks showed lower relatedness of benthic composition and coral community composition data. For this region, only estimated values of benthic composition were available (Table 11).

Table 11. ρ values from Spearman correlation analysis of relatedness of different multivariate analysis outcomes based on the same samples, from Farasan Banks (all data $\sqrt{}$ transformed)

<i>Benthic composition survey</i>	<i>Coral colony generic composition data</i>	
	colony density (per unit area, by taxa)	coral colony surface area (per unit area, by taxa)
visual estimates of all benthic groups	Adt = 0.27 (0.3%) Juv = 0.23 (0.8%)	Adt = 0.31 (0.1%) Juv = 0.20 (2.5%)

The three groups defined *a priori* as having shown mortality (see section 6.3), divided into 'low', 'moderate' and 'severe', showed no separation by groups when variables used were benthic composition estimates (Global $R = 0.06$, $p = 16\%$). This is contrary to the significant separation of samples by these factors observed when analysis was based on colony abundance data (by taxa) (see section 7.5.2.2; page 142). These results give a strong indication that coral community composition data from Farasan Banks sites showed a more effective means of discriminating mortality-effected sites than benthic composition estimates.

7.6 Taxonomic richness, equitability and dominance

This section examines the generic composition of adult coral communities between and within regions, analysing the extent to which differences in taxonomic composition may reflect different degrees of environmental disturbance.

7.6.1 Biodiversity indices

The number of genera within each reef site was similar across all sites within all regions, ranging from 17.6 (± 1.4) in the Granitic Seychelles to 21.4 (± 2.1) in Andavadoaka, Madagascar. Family numbers per site were even more consistent, ranging from 8.5 (± 0.5) at Granitic Seychelles sites to 10.0 (± 0.3) in the Farasan Banks, Saudi Arabia (Figure 58). The total number of taxa per region was markedly higher than the within-region site averages. Numbers ranged from 29 genera from 11 families (Toliara, Madagascar) to 51 genera from 17 families (Farasan Banks, Saudi Arabia).

The numbers of genera and families per region, along with corresponding Shannon Diversity (H') indices, are plotted for all survey regions in Figure 59. Values are calculated both as mean values for sites and for replicates (the latter with no subdivision by site) within each region.

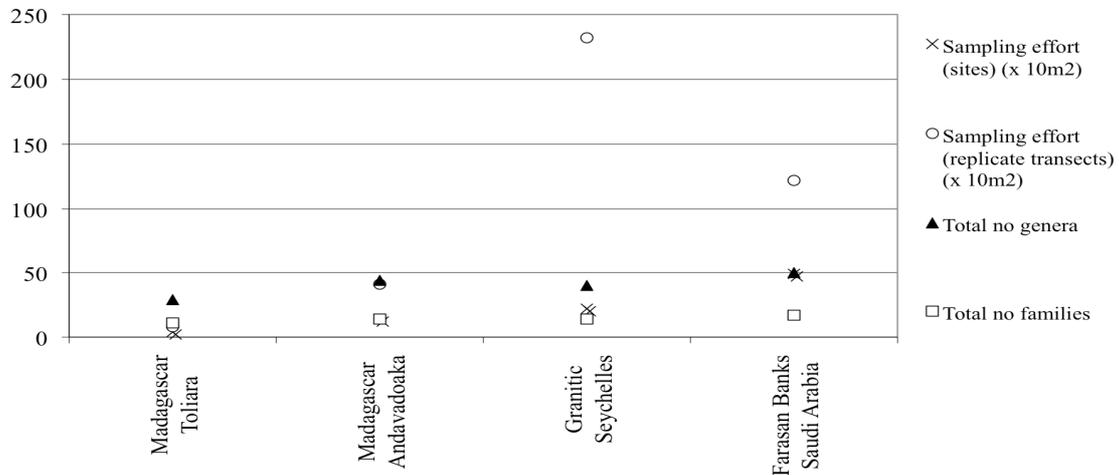


Figure 58. Total adult taxa recorded per region with sampling effort (defined by both the numbers of sites per region, and the total numbers of replicate transects (pooled sites) per region)

An approximately opposite trend in between-region differences is seen from the Shannon diversity index, whose values increase when taxa are present in equal numbers across sites. The relatively higher values of Shannon diversity compared to taxonomic richness from both Madagascar regions, for both generic and family diversities, indicate a higher evenness of taxa at these regions compared to the Granitic Seychelles and Farasan Banks (Figure 59). Standard deviation in H' is far higher in the Granitic Seychelles and Farasan Banks (0.59 and 0.49 respectively) than in the two Madagascar regions (0.16 and 0.27 respectively). The higher equitability of genera within the two Madagascar survey regions is further confirmed by the higher values of Pielou's evenness index (Figure 60).

The Simpson index (Figure 60) illustrates the dominance of taxa across sites and regions. Higher values correspond to coral communities that are dominated by one or few of the taxa present. Both the Granitic Seychelles and Farasan Banks, Saudi Arabia, show markedly higher dominance of families and genera than in the two Madagascar survey regions. This is caused by the dominance of *Porites* in both cases (section 7.2.2; page 113).

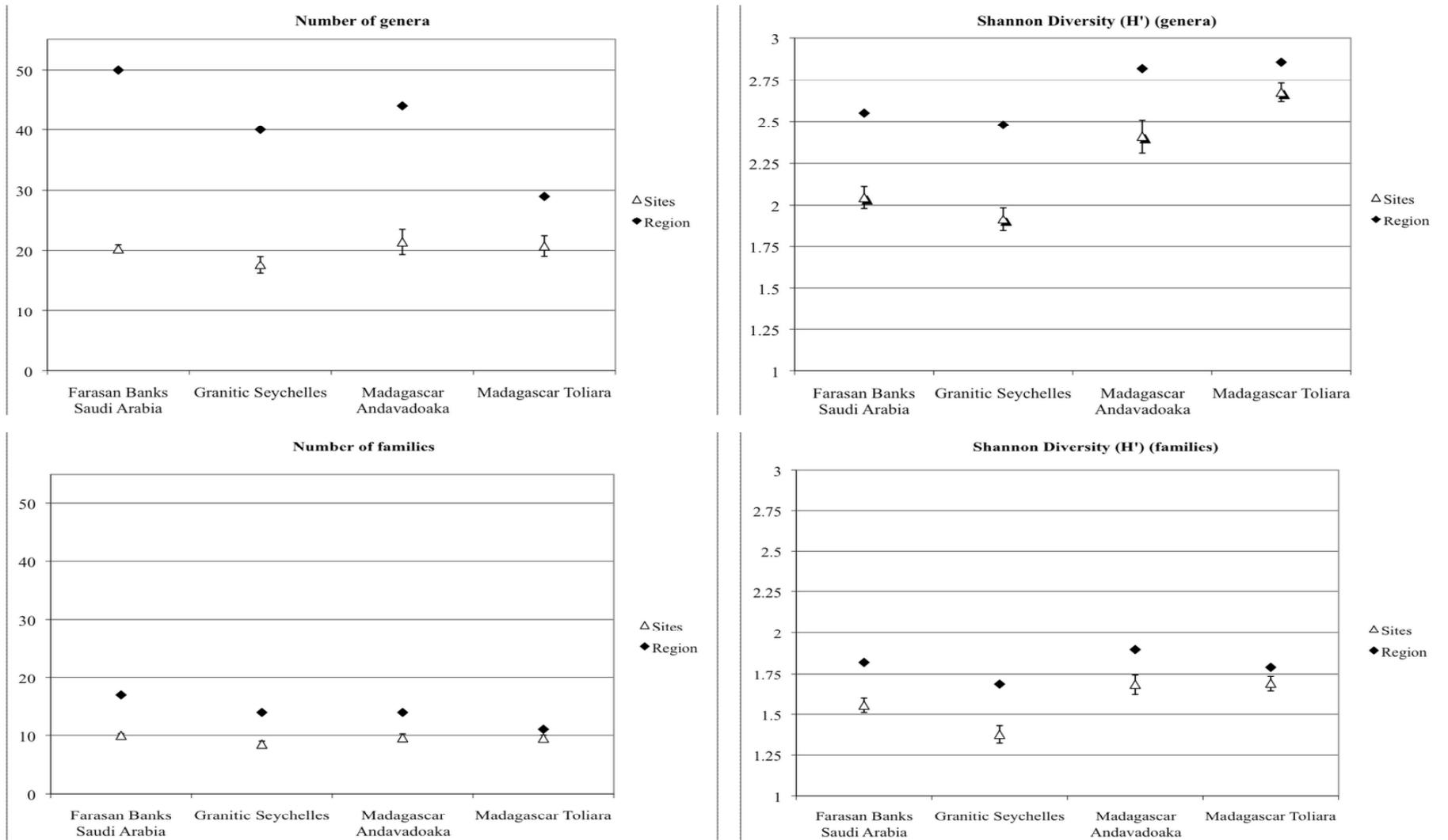


Figure 59. Total numbers of taxa and Shannon diversity indices by region for adult coral genera and families. Open triangles represent the mean \pm standard error across all individual sites within each region; filled squares indicate pooled data from all replicates per region (no subdivision of samples by reef site)

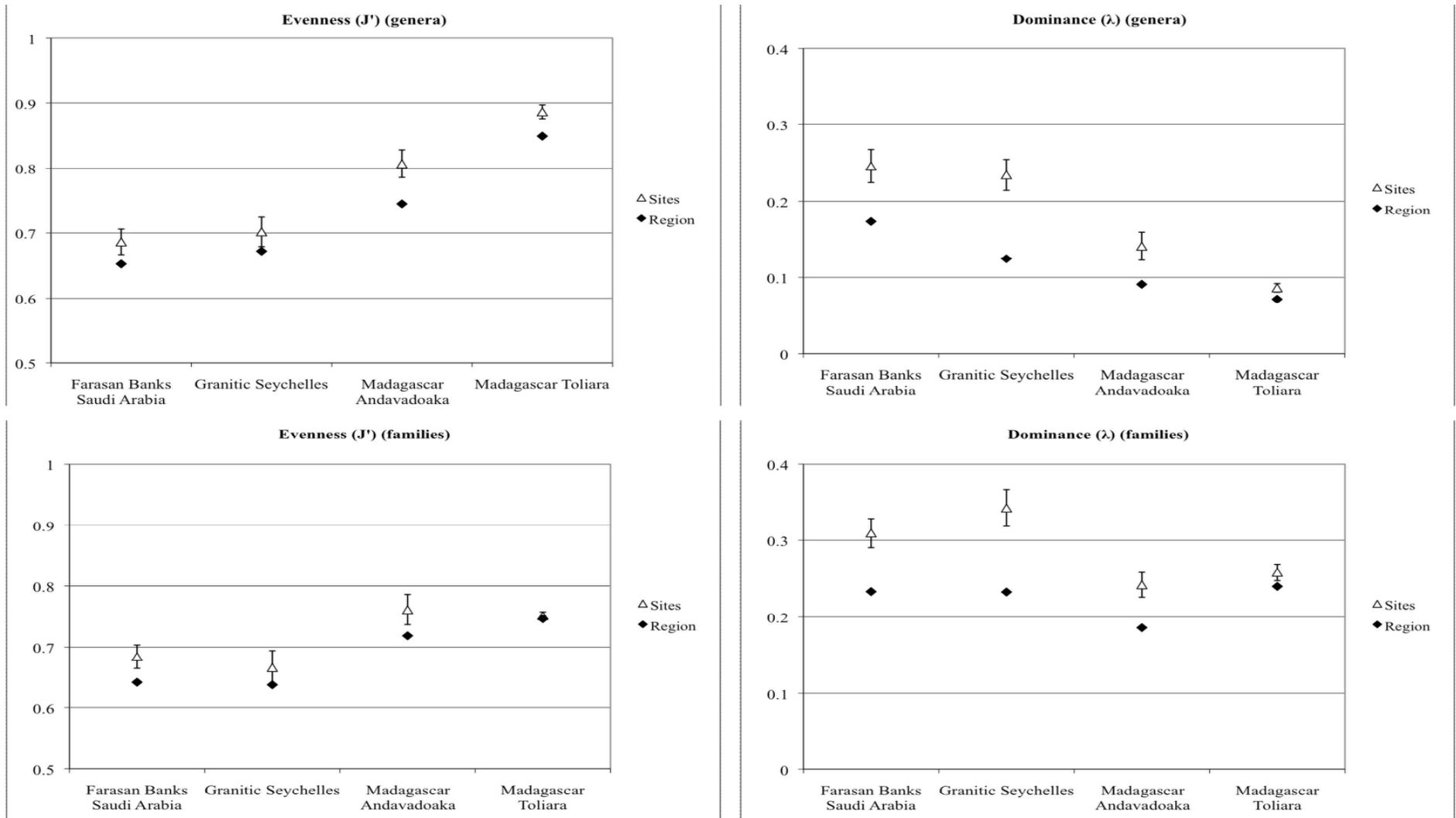


Figure 60. Simpson dominance index (λ) and Pielou's evenness index (J'), by region for adult coral genera and families. Open triangles represent the mean \pm standard error across all individual sites within each region; filled squares are indices derived from pooled data from all replicates per region (no subdivision by site)

7.6.2 Genus curves

7.6.2.1 Genus accumulation

Care should be taken not to misinterpret the significance of the differences in total genera recorded between regions since this is likely to be related to differences in sampling effort between sites (Figure 58; page 156, and see also section 7.5.2.4; page 147). The genus accumulation curves in Figure 61 plot the numbers of taxa recorded in adult coral surveys per region alongside sampling effort. These plots show the increasing total number of genera observed per region as sites are successively pooled, with the curves representing the average result of all within-region samples being entered in random order 999 times. Extrapolation of these curves suggests clearly different asymptotes, indicating that differences in genus richness between regions are not an artefact of sampling effort.

This approach is repeated basing the genus accumulation curves on individual survey replicates (with no subdivision by site), rather than by sites (mean of all replicates)(Figure 62). This is considered to be more accurate than pooling replicate samples within sites, since replicate numbers varied inconsistently between sites across the different survey regions. Nevertheless, regardless of the approach, these genus accumulation plots suggest that clear differences in genus richness between sample groups persist despite differences in sampling effort. In both cases, the Farasan Banks and Andavadoaka show higher generic richness than other regions, consistent with the taxonomic richness plots shown in Figure 59. Notably, when the plots are based on individual replicates, the Granitic Seychelles shows by far the lowest species richness of all regions.

Within-region differences in genus accumulation curves can also further validate the division of the Farasan sites into three groups based on the degree of observed mortality (Figure 63). In this case disturbance shows a clear effect on generic richness.

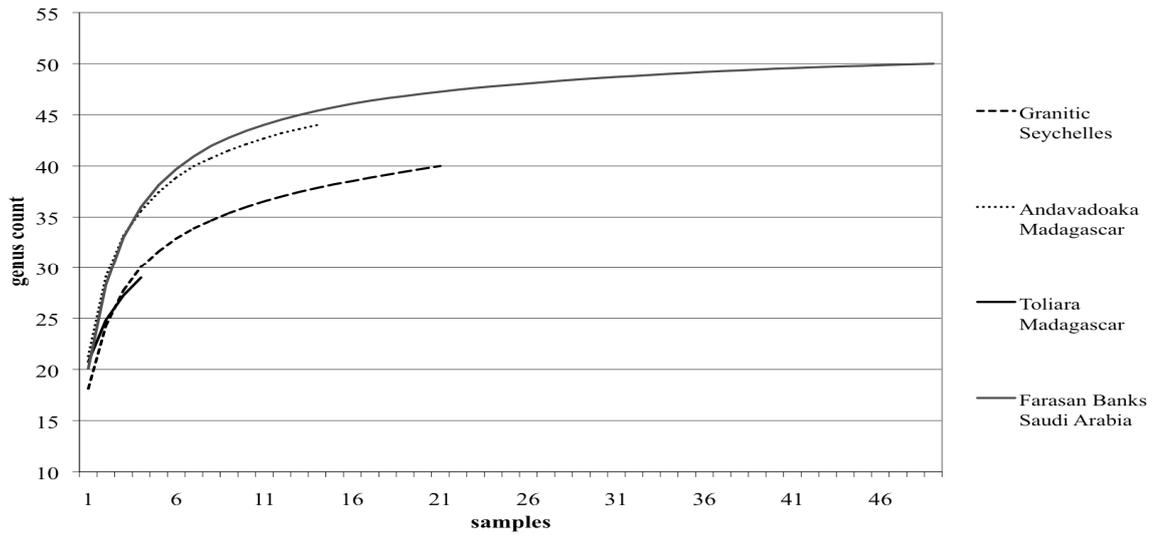


Figure 61. Genus accumulation plots (adult colonies), by survey region (samples are pooled replicates per survey site)

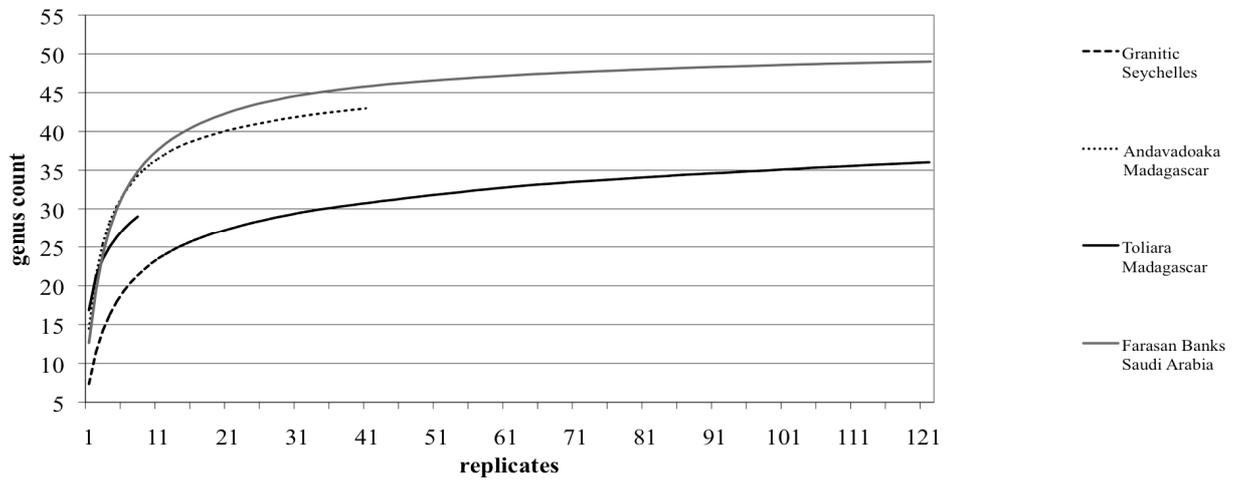


Figure 62. Genus accumulation plots (adult colonies), by survey region (all individual within-site replicates per region)

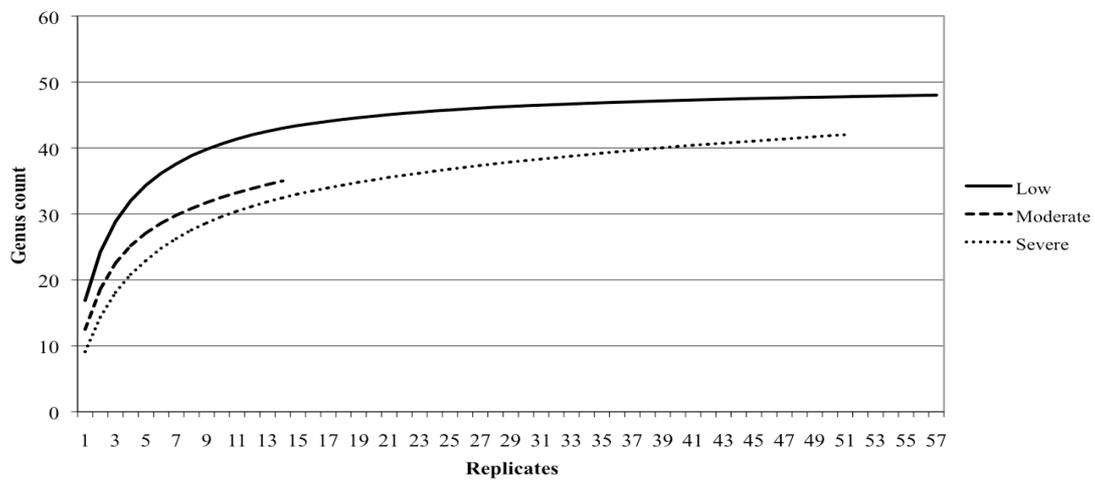


Figure 63. Genus accumulation plots (adult colonies) of samples within the Farasan Banks, divided by qualitative assessment of degree of coral mortality (all individual within-site replicates)

7.6.2.2 Geometric abundance

The geometric abundance curve (Figure 64) shows the number of genera represented by increasing numbers of colonies. The y-axis shows the number of genera falling into a geometric ($\times 2$) sequence of abundance classes, i.e. only 1 individual in the sample (class 1); 2-3 individuals (class 2); 4-7 individuals (class 3); 8-15 individuals (class 4), etc. Values are pooled data from all sites and samples within each region, standardised for sampling effort.

Undisturbed communities typically show many rare taxa, with a smooth geometric abundance curve whose mode is well to the left. Increasing disturbance generally reduces the number of rare taxa and increases the proportion of common taxa (Clarke and Warwick 2001).

Across all regions, communities extend over very few geometric abundance classes with broadly similar curves. There is a notable 'jaggedness' of the curves, scarcity of rare genera, and relatively high representation of geometric abundance class 3. The Farasan Banks and Andavadoaka show the smoothest geometric abundance curves indicating that these regions show larger numbers of rare taxa and a smaller proportion of common taxa.

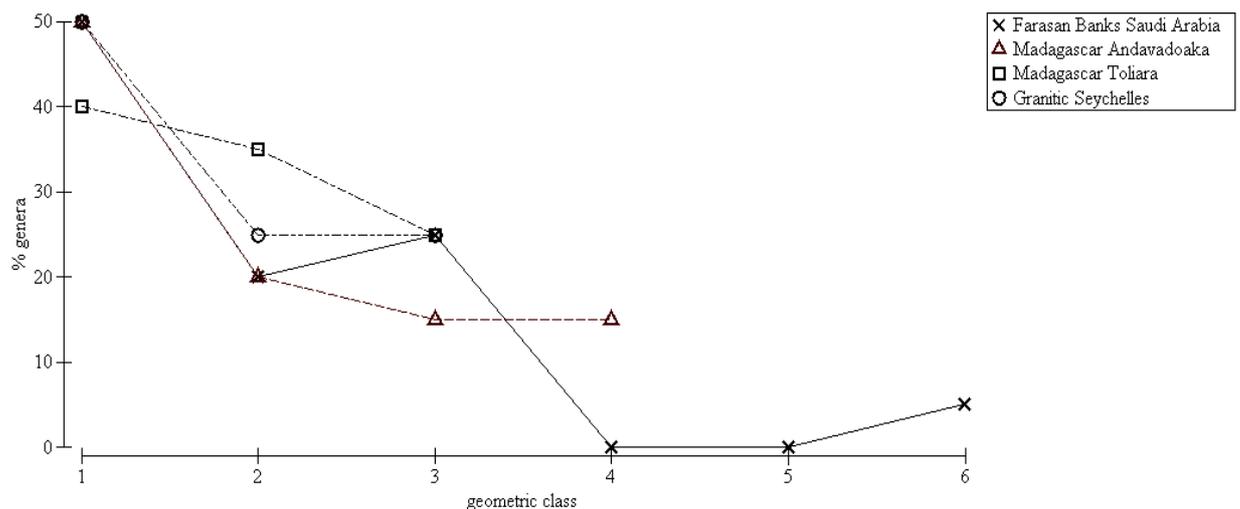


Figure 64. Plot of $\times 2$ geometric genus abundance classes for four survey regions

7.6.2.3 *k*-dominance

Figure 65 shows a *k*-dominance plot of adult genera from all sites analysed separately (pooled data from all replicates per site) for all four survey regions, with a total of 51 genera. The ranked abundances are expressed as a cumulative percentage of the total abundance of all genera, plotted against the relevant genus rank. Thus each curve represents the cumulative relative abundances of genera ranked in decreasing order. The x (rank) axis is logarithmically transformed to enable clearer visualisation of the commonest taxa. Genera are ranked in order of abundance on the x axis, with cumulative percentage dominance on the y axis. Figure 66 shows the same data with sites pooled to a single sample for each region, standardised to take account of variable sampling effort between regions.

From these two plots the Madagascar survey regions clearly show higher evenness (lower dominance), on account of their lower starting point on the y axis, consistent with the higher values of J' calculated for these regions from the same data. The Farasan Banks sites show the highest dominance, consistent with the higher values of λ calculated from the Simpson index, with the highest sites showing 80% numerical dominance of the coral community by one genus (*Porites*). An enlarged view of the dominance values >60% from Figure 66 illustrates the point that, although the Farasan Banks show the lowest equitability of genera on account of the numerical dominance of *Porites* (the curve starts higher than others on the y axis), this region also shows the highest taxonomic richness, since it exhibits the longest 'reach' along the x axis before the line attains cumulative 100% abundance (Figure 67).

Samples within regions can be pooled by factors defined *a priori*. For example, Figure 68 shows a *k*-dominance plot of adult genera in Andavadoaka, Madagascar, with sites pooled to each geomorphological class of reef as defined by Nadon *et al.* (2007) (near shore fringing reef, lagoonal patch reef and offshore fringing/barrier reef), adjusted for sampling effort.

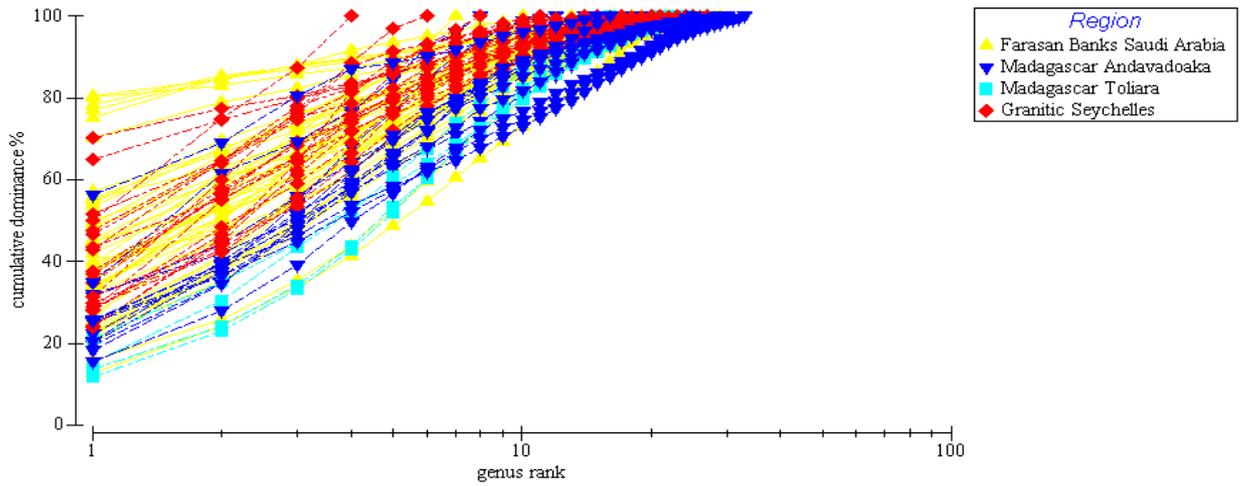


Figure 65. *k*-dominance curves based on colony abundance data by genera; mean values for all sites, all regions

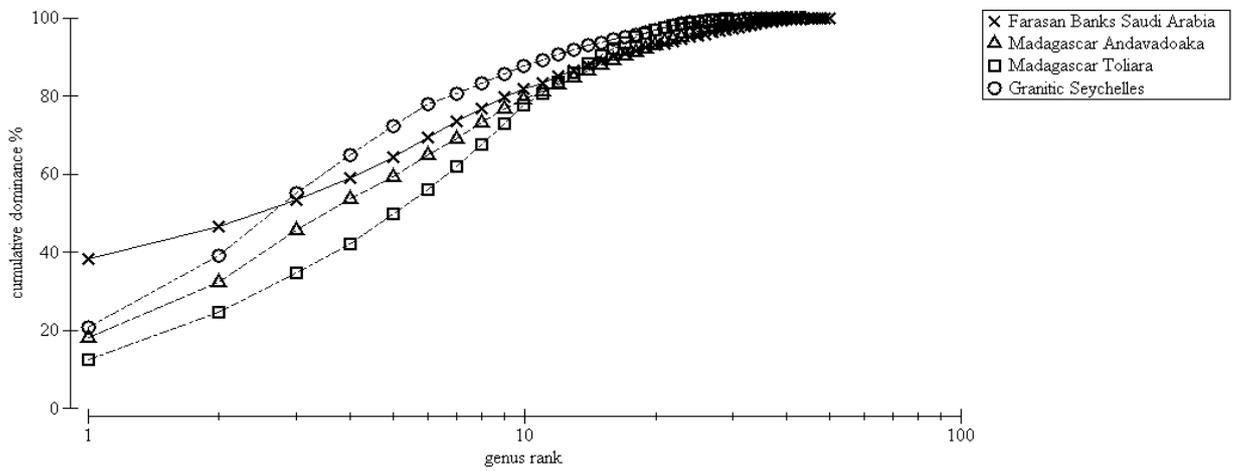


Figure 66. *k*-dominance curves based on colony abundance data by genera; mean values for all sites within each region

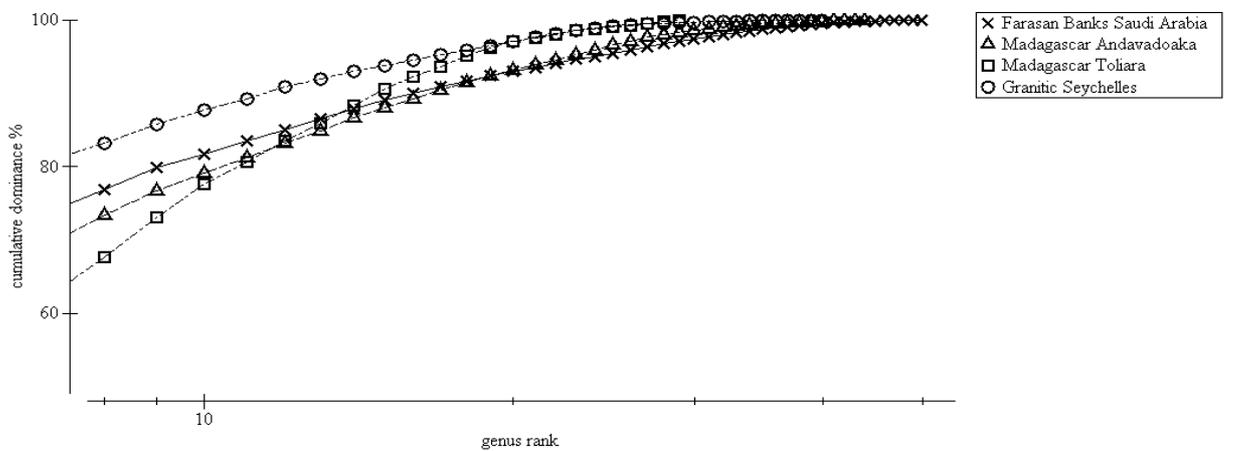


Figure 67. Enlargement of *k*-dominance curves (>60%) from the *k*-dominance curves for colony abundance data (by genera) shown in Figure 66

Here the more degraded near shore sites, despite being characterised by lower coral cover (section 6.4; page 86) show higher equitability and higher richness of genera, with the 'healthier' patch reef sites showing the highest levels of generic dominance. Figure 69 shows *k*-dominance curves from sites within the Farasan Banks, based on mean values across all replicates grouped by the degree of mortality observed. Sites heavily affected by mortality show marginally lower generic richness but substantially lower genus equitability than unaffected sites. This indicates that sites experiencing mortality show higher levels of generic dominance than undisturbed reefs.

Differences between cumulative *k*-dominance curves were plotted individually from all sites and regions across sample groups using the DOMDIS routine to calculate the 'distance apart' of all pairs of samples (Clarke 1990). These tests were carried out on raw sample data for each sample group (individual sites, as displayed in Figure 65), rather than on pooled data for each region or factor group (as displayed in Figure 66 to Figure 70).

ANOSIM testing for the significance of differences between survey regions, based on the resulting DOMDIS dissimilarity matrix, showed differences in the cumulative relative abundance of genera between regions, with $R = 0.21$ under the hypothesis of no between region difference ($p < 0.1\%$). The *R* statistic is slightly depressed by the close pairwise similarity of samples between the two Madagascar regions, as well as between the Granitic Seychelles and Farasan Banks survey regions, but given the large sample size this low Global *R* value may be considered significantly different from zero.

Repetition of the same routine for within-region analyses showed no significance of differences between *k*-dominance curves from samples from the three geomorphological classes of reef within the Madagascar survey regions, despite the different curve shapes observed for pooled samples in Figure 68 ($R = 0.172$, $p = 3.1\%$). Within-region site comparisons from the Granitic Seychelles also failed to show any significance based on geomorphology ($R = 0.11$, $p = 9\%$).

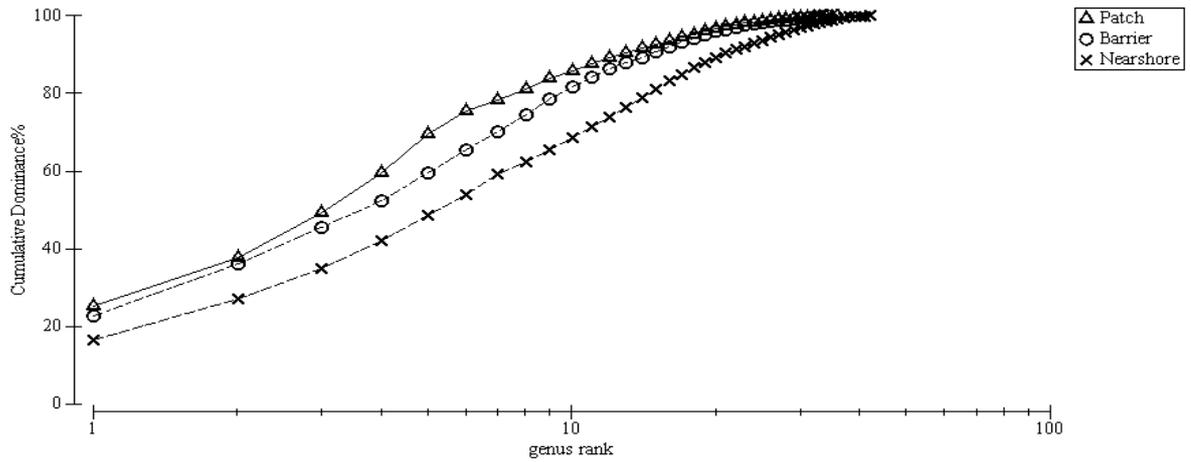


Figure 68. *k*-dominance curves based on colony abundance data by genera; Andavadoaka, Madagascar, mean values for all replicates based on geomorphological reef class

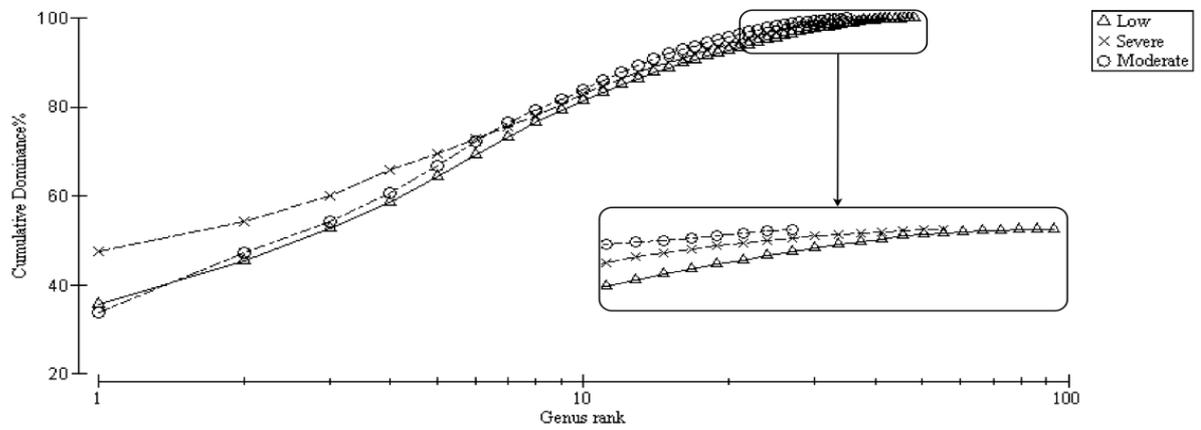


Figure 69. *k*-dominance curves based on colony abundance data by genera; Farasan Banks, Saudi Arabia, mean values for all replicates based on degree of observed coral mortality. Inset shows enlarged view of upper 10%



Figure 70. Non-metric MDS ordination of sites from the Farasan Banks, Saudi Arabia, based on dissimilarity matrix from DOMDIS routine, showing between-site similarities of *k*-dominance curves. Sites labeled based on observed incidence of coral mortality

However, within-region site comparisons from the Farasan Banks showed highly significant differences in *k*-dominance curves between the groups of sites that had experienced mass mortality and unaffected sites ($R = 0.22$, $p = 0.1\%$)(moderate and severe categories combined to 2 categories of presence/absence mortality)(Figure 70). Mortality-affected sites broadly separate from unaffected reefs, as a result of the significant differences in cumulative relative abundance of genera between affected and unaffected reefs.

7.6.2.4 Abundance/area curves (AAC)

Figure 71 shows separate *k*-dominance curves for genus abundances and surface areas on the same axes. These abundance/area curves (AAC) are based on the *k*-dominance abundance/biomass curves (ABC) (Warwick 1986). The assumption of the ABC plot is that the distance between the abundance and biomass curves of *k*-dominance plots represents the degree of environmental disturbance to a macro-benthic community (see methods section 5.4; page 76). In this case biomass data are substituted by colony surface area data.

The ABC hypothesis states that in a healthy benthic community, the biomass (substituted here by surface area) curve should lie above the abundance curve along its entire length, with the two curves coming closer together, and eventually transposing, with increasing disturbance. Data shown in Figure 71 are from Granitic Seychelles sites only, with samples pooled and standardised by the Jennings (1996) geomorphological classes.

The abundance and surface area *k*-dominance curves from granite reef sites in the Granitic Seychelles (Jennings 1996) are considerably closer together than those from other reef types. The closer proximity of the curves at these sites is likely to be a result of the smaller colony sizes found on the granitic reefs rather than disturbance at these sites, since separate analyses showed a higher abundance of colonies on granitic reefs in this region (section 6.2).

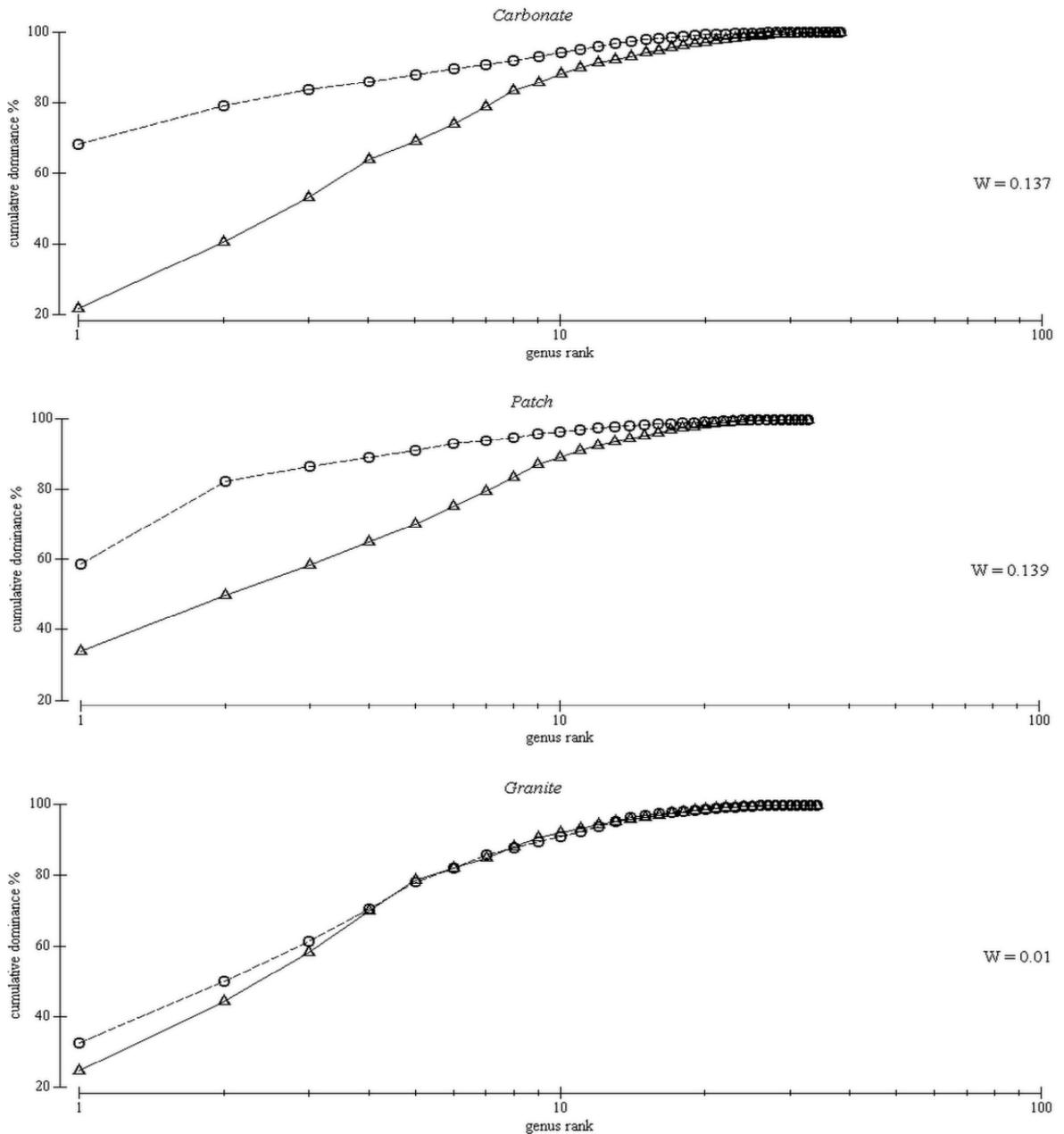


Figure 71. “AAC” k -dominance curves for genus surface area (circles) and abundance (triangles) for the three geomorphological classes of reef surveyed in the Granitic Seychelles. Pooled data for each reef class

Owing to the large number of reef sites surveyed in this study, AAC plots cannot be usefully presented for every sample or group of samples based on factors. The W index (Clarke and Warwick 2001), taking a value between -1 and 1, represents the difference between the abundance and area curves, and provides a means of conveniently comparing AAC curves between sites and groups of sites, enabling testing for differences between samples.

Figure 72 shows the differences in mean W values across the four survey regions, as well as between groups of sites within the Granitic Seychelles grouped by reef geomorphology, based on Jennings (1996). ANOVA testing for significance of differences in W between three regions for which sufficient samples were available (Madagascar Andavadoaka, Granitic Seychelles and Farasan Banks) showed weak significance of between-region differences ($p = 0.04$) however non-homoscedasticity of Andavadoaka samples relative to the other regions further constrains the significance of this result.

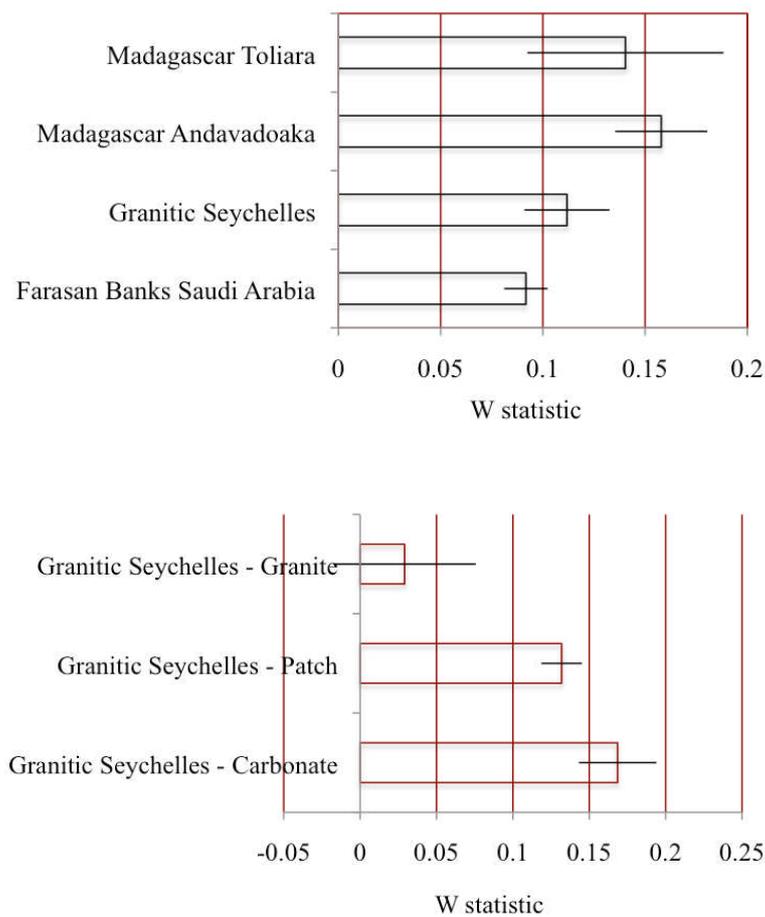


Figure 72. Mean W values (\pm standard error) from all samples from each of the survey regions (above) and from samples within the Granitic Seychelles pooled by reef geomorphological class (below)

8 Methodological comparisons

This section compares different methodological approaches to monitoring coral communities. The effectiveness of using ultraviolet light to improve juvenile coral surveying is examined, and the effect of monitoring only a subset of the overall coral community as target 'indicator genera' is investigated.

8.1 Ultraviolet juvenile coral census

For consistency, all data on juvenile corals presented in above analyses were collected without the use of underwater UV lighting, unless stated otherwise. Use of UV in surveying juvenile corals in the Farasan Banks, Saudi Arabia, shows a pronounced increase in abundance of juvenile corals. Across all sites and replicates, the technique resulted in a 36% increase in the measured abundance of juvenile colonies (≤ 10 cm maximum diameter) from 66.1 (± 2.8 SE) to 89.8 (± 3.4 SE) colonies m^{-2} . This difference increases with smaller colony size, especially below 4 cm maximum diameter. These increases in colony abundance equate to a 10% increase in overall juvenile colony surface area per unit area across all size categories (Figure 73).

Across all replicates and samples in this survey region (pooled taxa), the UV technique resulted in a decrease in the recorded median colony size from 4 cm (without UV) to 3 cm (with UV), equivalent to a decrease in mean colony size from 4.2 cm (± 0.05 SE) to 3.7 cm (± 0.05 SE). The differences in juvenile colony size frequency distributions were highly significant (two-sample T-test of transformed data $P < 0.000$, $DF = 4399$).

The size frequency distribution of the additional colonies (only) detected using UV also differed significantly from those identified without UV, their mean size being 2.1 cm (± 0.07 SE), compared to 4.2 cm (± 0.05 SE) for non-UV 'white light' colonies (two-sample T-test of transformed data $P < 0.000$, $DF = 1319$).

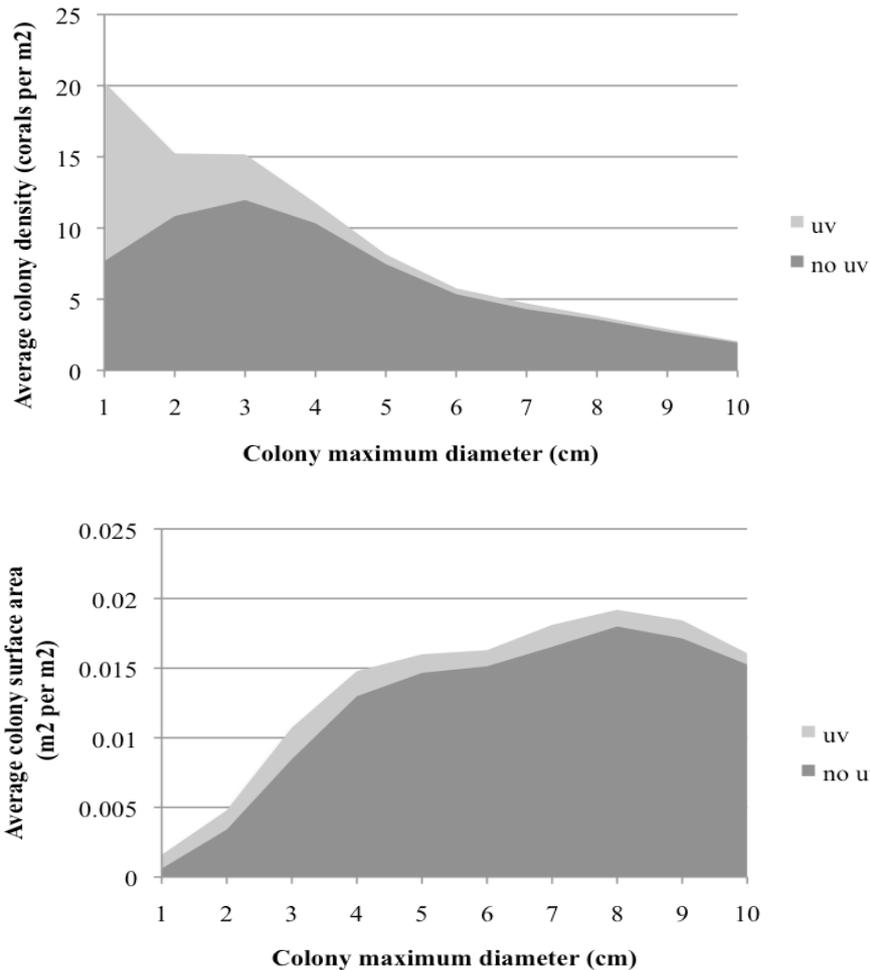


Figure 73. Effect of use of ultraviolet lamp on surveys of juvenile corals at the Farasan Banks, Saudi Arabia. Plots show mean colony density and surface area per m² juvenile colony size class, standardised across all samples and replicates in this survey region (dark area = CCCR method; light area = all taxa)

8.2 Sampling only CCCR target genera, grouped within size bins

CCCR methods record a reduced sub-set of the coral fauna; this is becoming a widespread technique. Removal from the present data of 'non target' CCCR taxa enables analysis of the effect of this reduction on size frequency distribution, taxonomic composition and taxonomic richness.

8.2.1 Effect on coral community size frequency distribution

Figure 74 and Figure 75 show the effect on colony abundance and surface area values of limiting the number of sampled coral genera to the CCCR subset of 21 genera. Across all regions surveyed, juvenile and adult abundance per unit area are reduced by 16% and 8% respectively, equivalent to a reduction in total surface area of 14% and 12% respectively. In Andavadoaka, Madagascar the

surface area reduction was 34% in sampled adult colony surface area, in this case mainly due to the exclusion of *Diploastrea*.

Despite these differences in both colony density and surface area, the CCCR sampling approach caused no significant change to overall community size frequency distribution. Pooled data resulting from the different approaches (all samples, all regions), had identical mean colony size values (to 2 decimal places)(two-sample T-tests of transformed colony data from the two datasets: $P = 0.98$, $DF = 35755$ for adult data; $P = 0.33$, $DF = 10487$ for juvenile data).

8.2.2 Effect on multivariate taxonomic composition analyses (taxa by samples)

The multivariate analyses of genus-by-sample matrices (section 5.3; page 70) were repeated using the CCCR corals alone, for comparison. Resulting MDS ordinations show similar trends between samples and regions to those obtained from analyses using all taxa (section 7.5.2.1; page 137). 2nd stage MDS analyses illustrate the relatedness of the outcomes of multivariate analyses based on this reduced community compared to analyses using the full complement of coral data (section 5.3.5; page 73). Resulting MDS ordinations (Figure 76) show close agreement.

Similar concordance is seen for within-region comparisons of 'full taxa' versus CCCR corals. For example, analysis of differences between samples from the Farasan Banks based on the degree of observed coral mortality (using adult colony density data across all replicates), shows almost identical significance of sample groupings (ANOSIM Global $R = 0.27$, compared to $R = 0.26$, $p < 0.1\%$).

These observations indicate that the genera selected by the CCCR approach are sufficient to account for the significant separation of groups of samples, and for the similarities of samples within groups. Thus surveying these target taxa only is able to provide an accurate means of discriminating samples between and within regions based on generic composition.

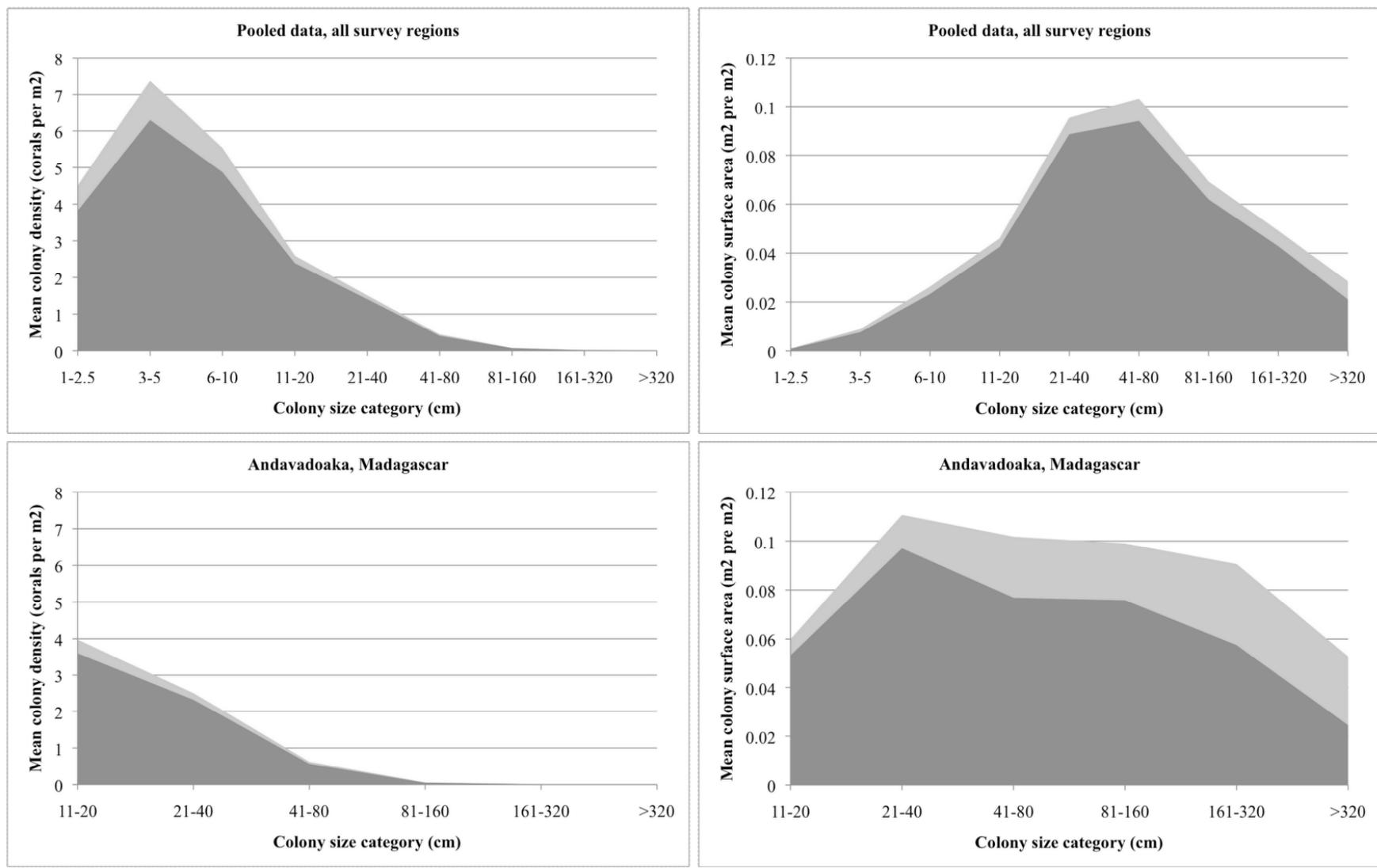


Figure 74. Mean colony density (left) and surface area (right) of corals based on all regions and samples (above), and Andavadoaka, Madagascar only (below), showing effect of exclusion of non-target genera on density and surface area values (dark area = CCCR method; light area = all taxa)

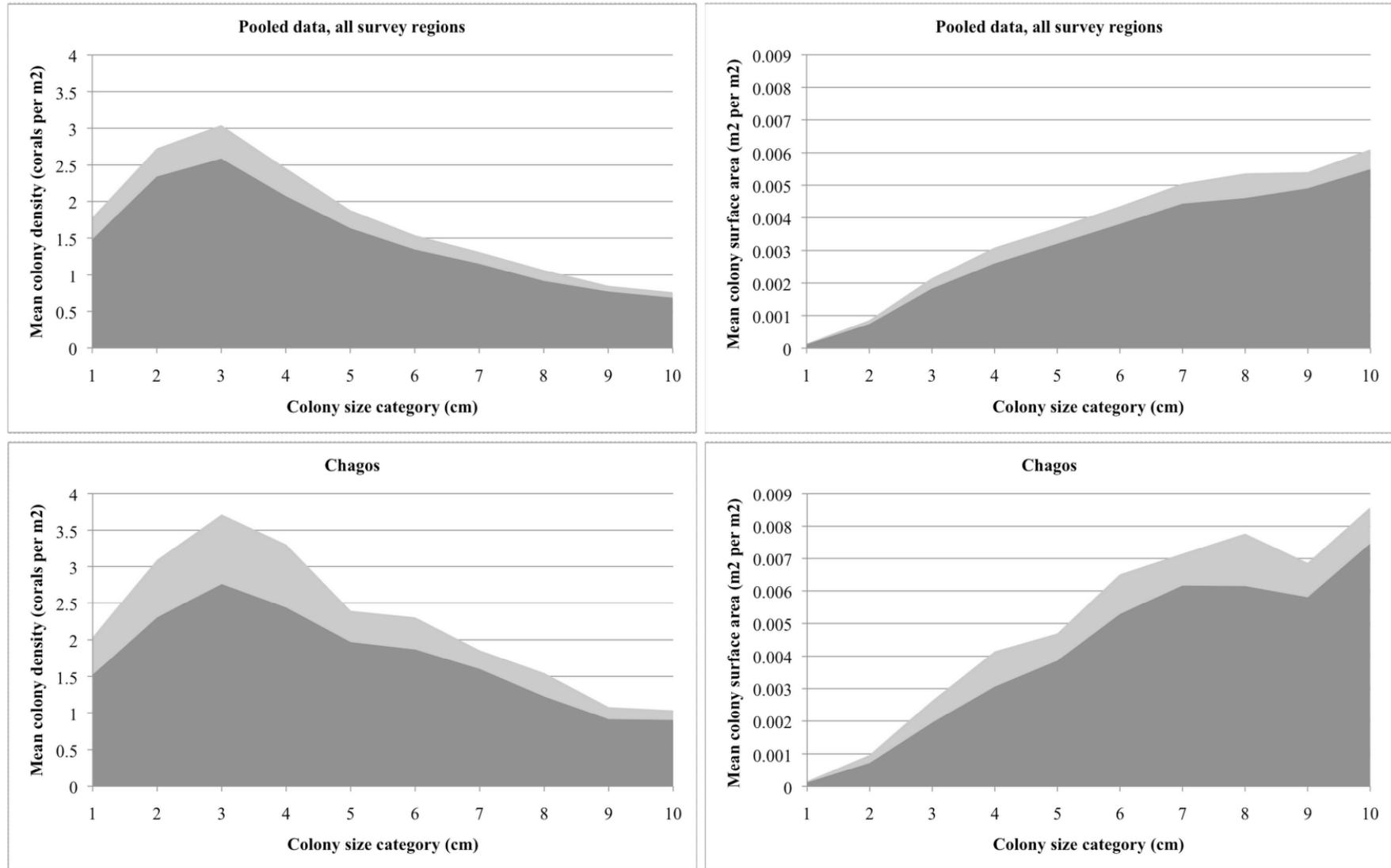


Figure 75. Mean colony density (left) and surface area (right) of juvenile corals based on all regions and samples (above), and Chagos only (below), showing effect of exclusion of non-target genera on density and surface area values (dark area = CCCR method; light area = all taxa)

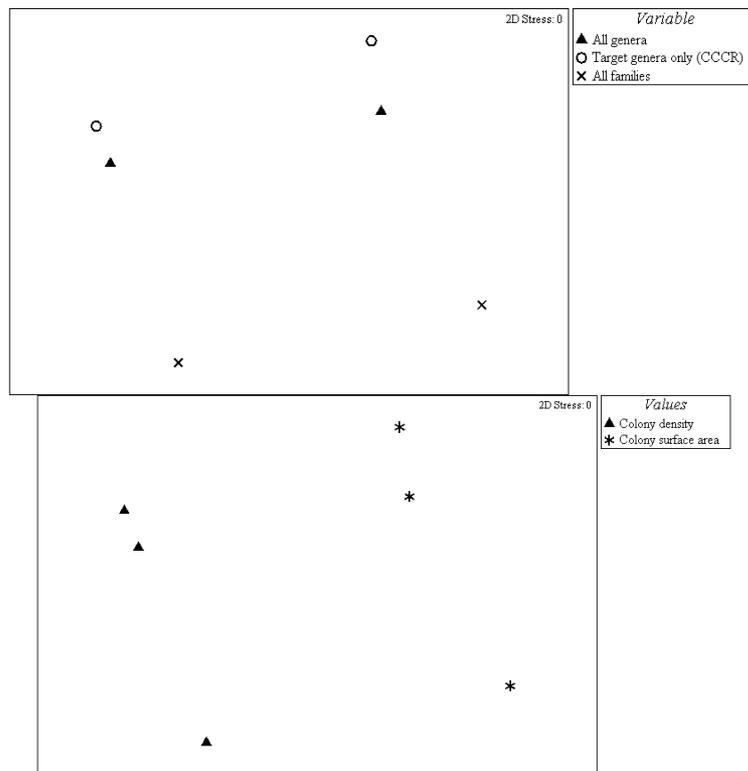


Figure 76. 2nd stage MDS ordination of relatedness of different multivariate analysis outcomes, showing impact of changing values and variables (all families, all genera, and truncated target (CCCR) genera)

8.2.3 Effect on taxonomic richness

The effect of generic reduction when using CCCR taxa only was examined. In the case of the Farasan Banks, the CCCR approach reduces taxonomic richness from 51 to 20 genera, which inevitably constrains the sensitivity of between-sample comparisons based on taxonomic richness of corals. Figure 77 shows genus accumulation curves on all replicate samples of adult corals from the Farasan Banks, Saudi Arabia, after reduction of original data to the 21 target taxa (replicate samples separated based on the degree of observed coral mortality).

Aside from the generic reduction, accumulation plots from the reduced community of target taxa show convergence towards the same number of genera after fewer samples. Thus because this lower y-axis asymptote does not give an accurate indication of total generic richness, it cannot show potential impacts of disturbance on generic richness.

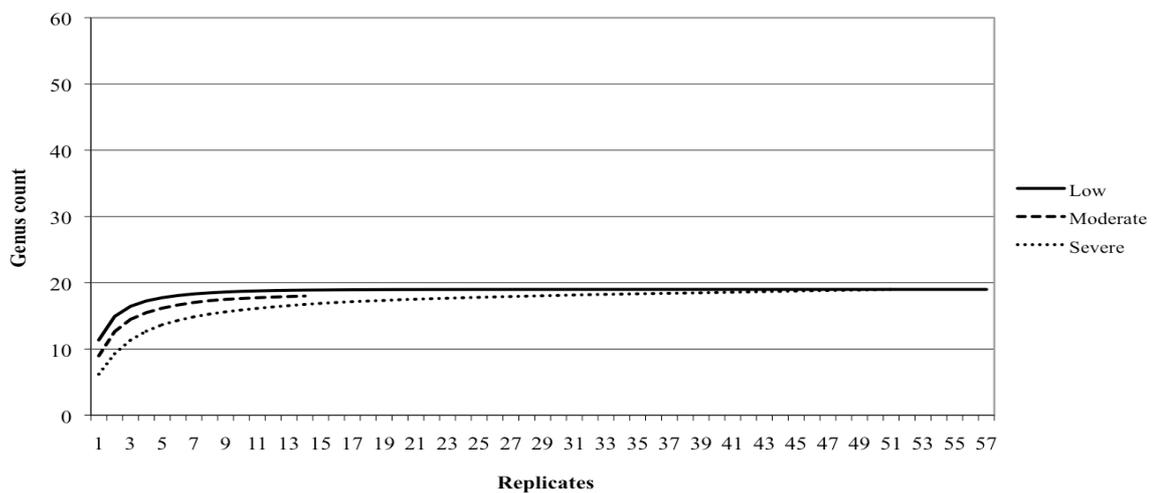
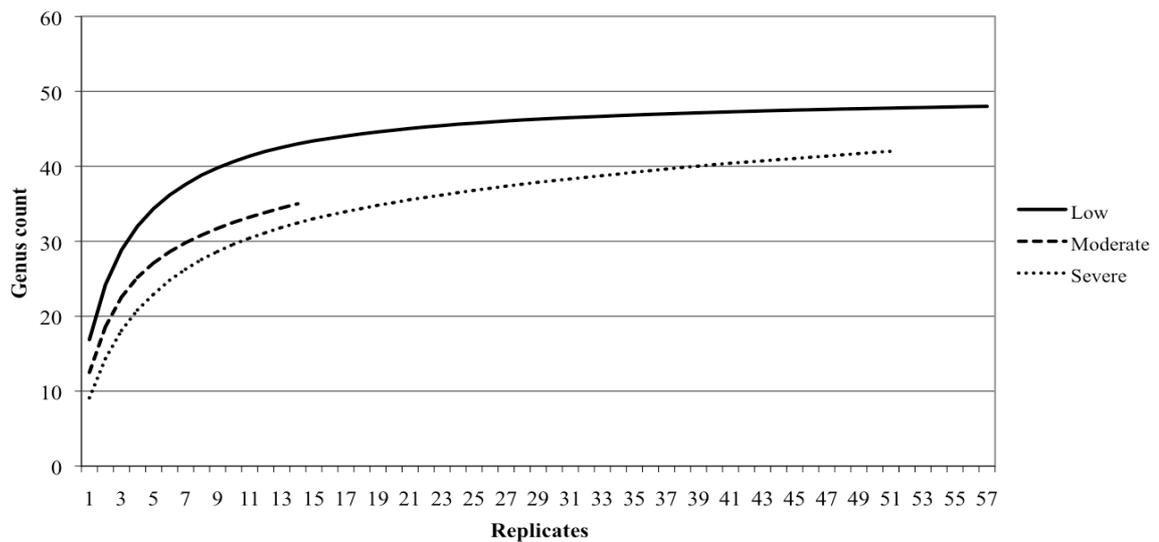


Figure 77. Genus accumulation plots (adult colonies) of samples within the Farasan Banks, divided into three categories of coral mortality (all individual within-site replicates), showing difference between sampling all taxa (above) and sampling CCCR target genera only (below)

Lower equitability of genera is another consequence of using the restricted CCCR suite. Figure 78 shows the result of using the CCCR suite only on *k*-dominance curves for samples from the Farasan Banks.

The true reduction in generic richness that was shown to result from mortality (based on analyses using all taxa) cannot be detected when only CCCR taxa are used. Moreover these curves show a lower equitability of remaining taxa across samples. This increased level of generic dominance is true across all three levels of observed mortality (Figure 78).

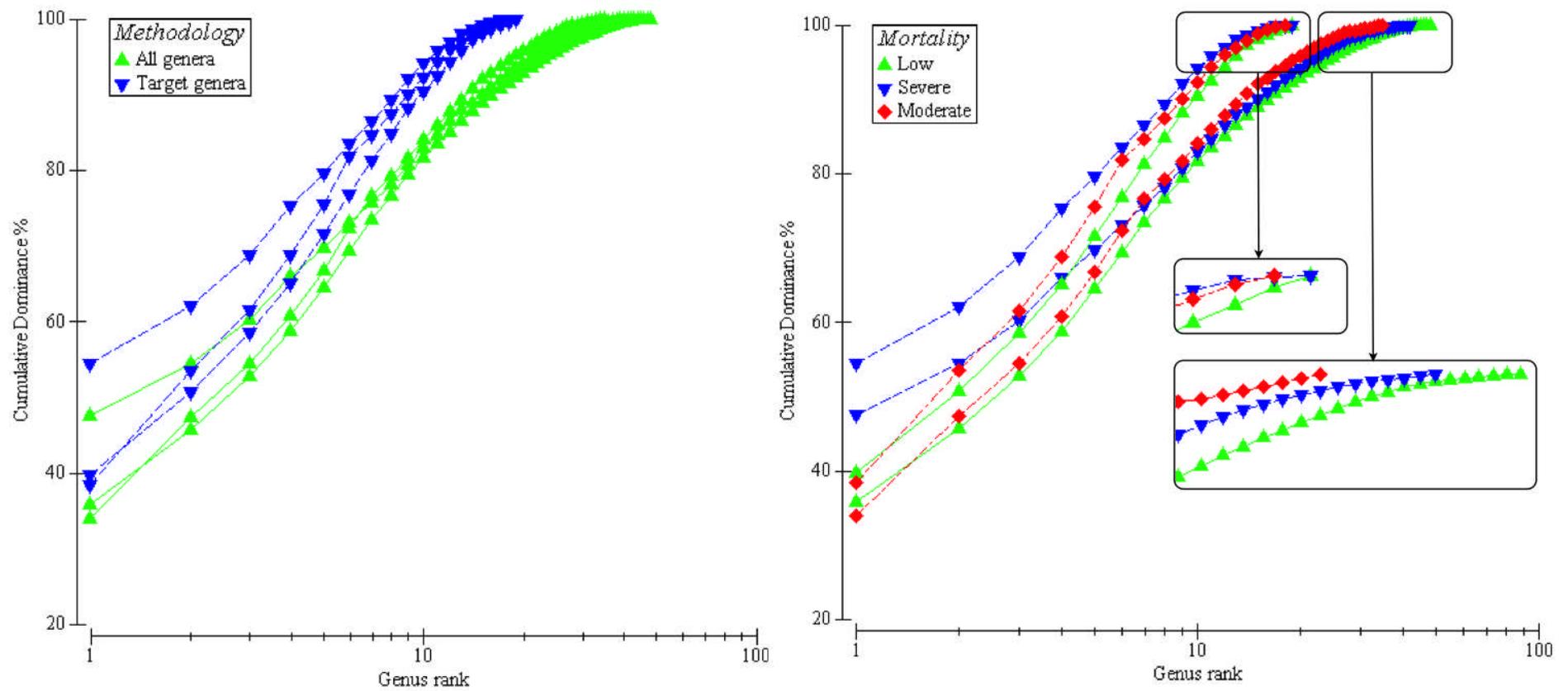


Figure 78. *k*-dominance curves based on colony abundance data by genera; Farasan Banks, Saudi Arabia, showing effect of reducing taxa to CCCR target genera only. Mean values for all replicates, divided into three categories of coral mortality

8.3 Identifying 'indicator' genera as subset of coral community

In order to establish whether differentiation of samples based on severe/low mortality categories could be obtained using different subsets genera, Farasan Banks data (all genera) were re-analysed. Samples identified with the mortality factor 'moderate' were removed, since prior analyses showed these not to be significantly different to the 'severe' category.

Removal of genera comprising less than 5% of the number of colonies within at least one sample site then resulted in a reduction from 51 to 38 genera, with the elimination of the following taxa: *Alveopora*, *Coscinarea*, *Gyrosmlia*, *Halomitra*, *Leptoria*, *Oulophyllia*, *Oxypora*, *Pachyseris*, *Physogyra*, *Podabacia*, *Psammocora*, *Siderastrea* and *Trachyphyllia*. A triangular model matrix (Clarke and Warwick 2001) was produced on the remaining 2 levels of the mortality factor (severe/low), recording 0s between samples in the same group (severe or low mortality), and 1s between samples in different groups.

BVSTEP analysis carried out on transformed data from the sample-by-genus matrix (all samples, reduced genera) produced a subset of 12 genera whose similarity matrix correlated most closely with that of the model matrix ($\rho = 0.4$): *Acanthastrea*, *Acropora*, *Diploastrea*, *Echinophyllia*, *Favia*, *Hydnophora*, *Montastrea*, *Pavona*, *Plerogyra*, *Porites*, *Stylophora* and *Symphyllia*.

MDS ordination of samples based on these 12 genera shows improved separation and grouping of samples based on the factors (low/severe mortality). This is, however, to be expected, since these genera were selected in order to maximise the separation between samples based on this factor, but, notably, only five of these genera are target taxa included in the CCCR protocol: *Diploastrea*, *Symphyllia*, *Plerogyra*, *Montastrea* and *Echinophyllia*.

The results of this statistical approach to selecting genera responsible for between-sample groupings based on the degree of mortality observed should not be interpreted as an endorsement of the use of these selected genera as indicator taxa. Different circumstances and areas would require similar,

appropriate treatment, depending on factors such as vulnerability to bleaching stress, and contribution of each genus to overall coral cover. Taxa differentiating these groups of samples are likely to differ from those driving between-sample differences in other regions.

9 Sea surface temperatures

Trends in SST over the past 11 decades are shown for all eight survey regions (Figure 79). A distinct warming trend is clear across all regions. A consistent marked difference in SST between regions is also apparent; the coolest being the highest latitude southern Madagascar sites, the warmest being the southern Red Sea and equatorial central Indian Ocean.

Figure 81 shows differences between the annual mean SST (calculated as the mean of 12 monthly values) and the 1900-1950 inter-annual mean SST for each region, over the six decades since 1951, with the 10-year moving mean superimposed on the data. All regions show a distinct warming trend with increasingly positive anomalies in the southern Madagascar and Seychelles survey regions. At the seven survey regions located in Saudi Arabia, Seychelles, Southern Madagascar and Chagos, either five or six of the ten most positive mean SST anomalies relative to the 1900-1950 interannual mean SST have all taken place in the past decade.

Monthly SST trends since 1980 are shown in Figure 82. These plots illustrate the considerable inter-regional differences, such as much higher seasonality and amplitude in the higher latitude regions in southern Madagascar and the Red Sea, as is emphasised by the higher standard deviations in annual temperature for these regions shown in Figure 80. Chagos shows a markedly lower annual standard deviation in SST than other regions, (approximately one fifth of that seen at the Farasan Banks) followed by the Seychelles and northwest Madagascar regions. There is no evident trend in changing standard deviation across the 108-year data set.

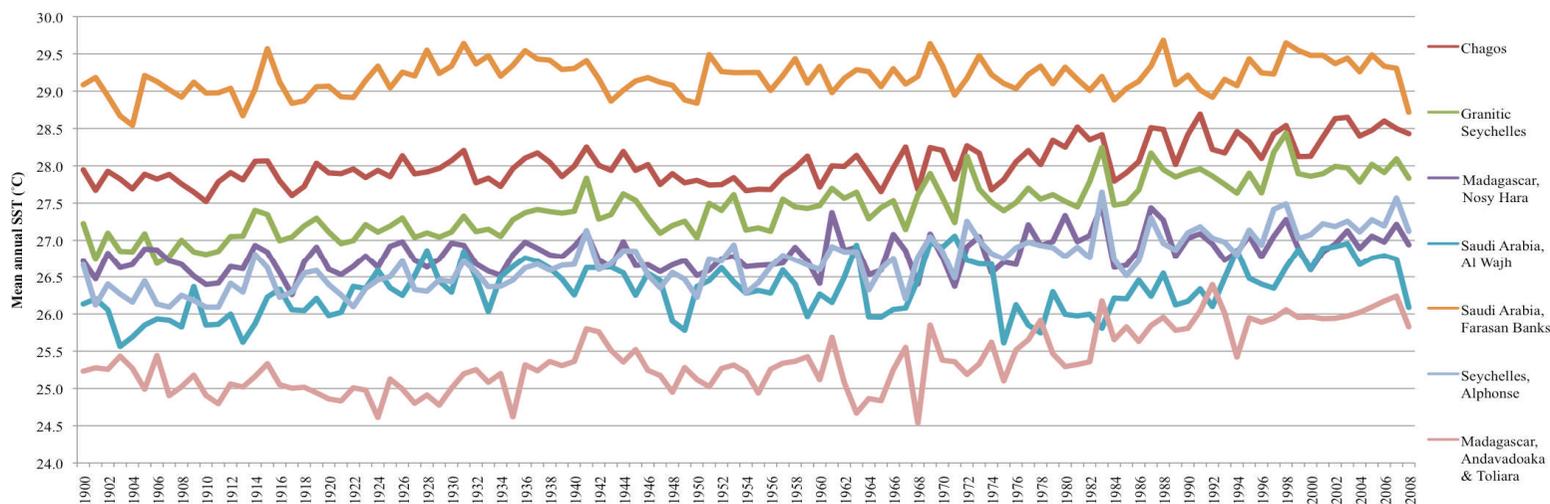


Figure 79 - mean annual SST, based on monthly values, 1900 - 2008

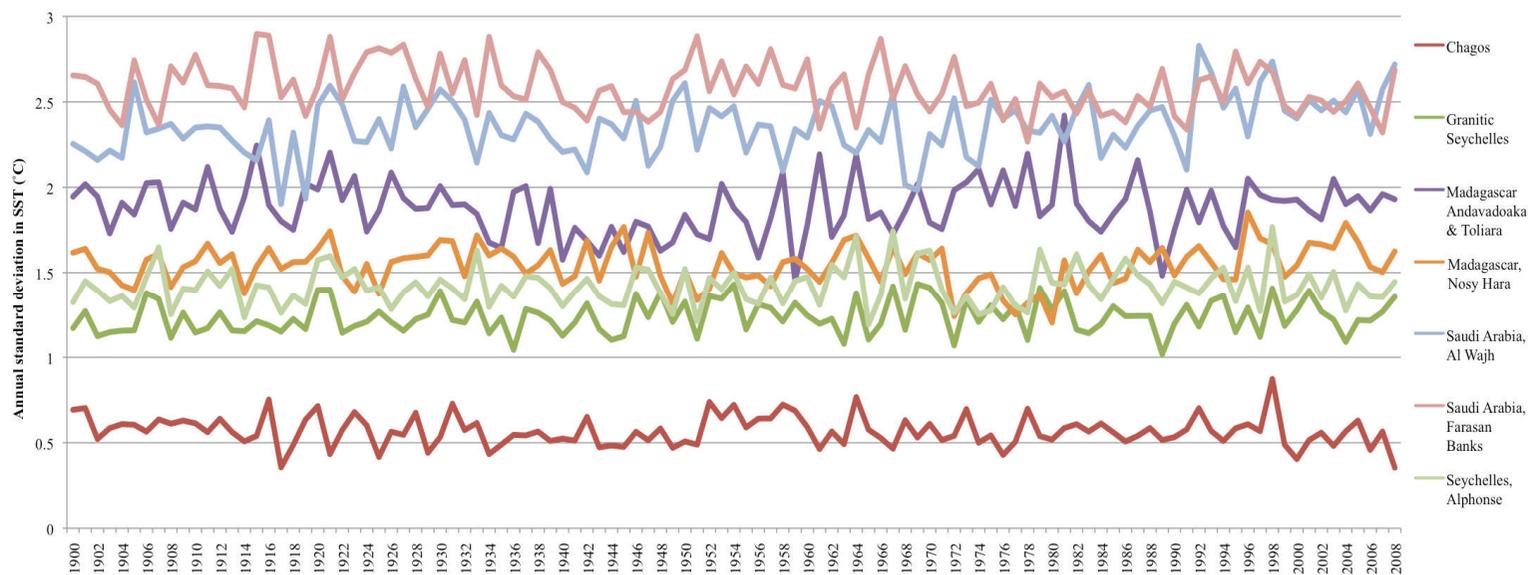


Figure 80. Mean annual standard deviation in SST, based on monthly values, 1900 - 2008

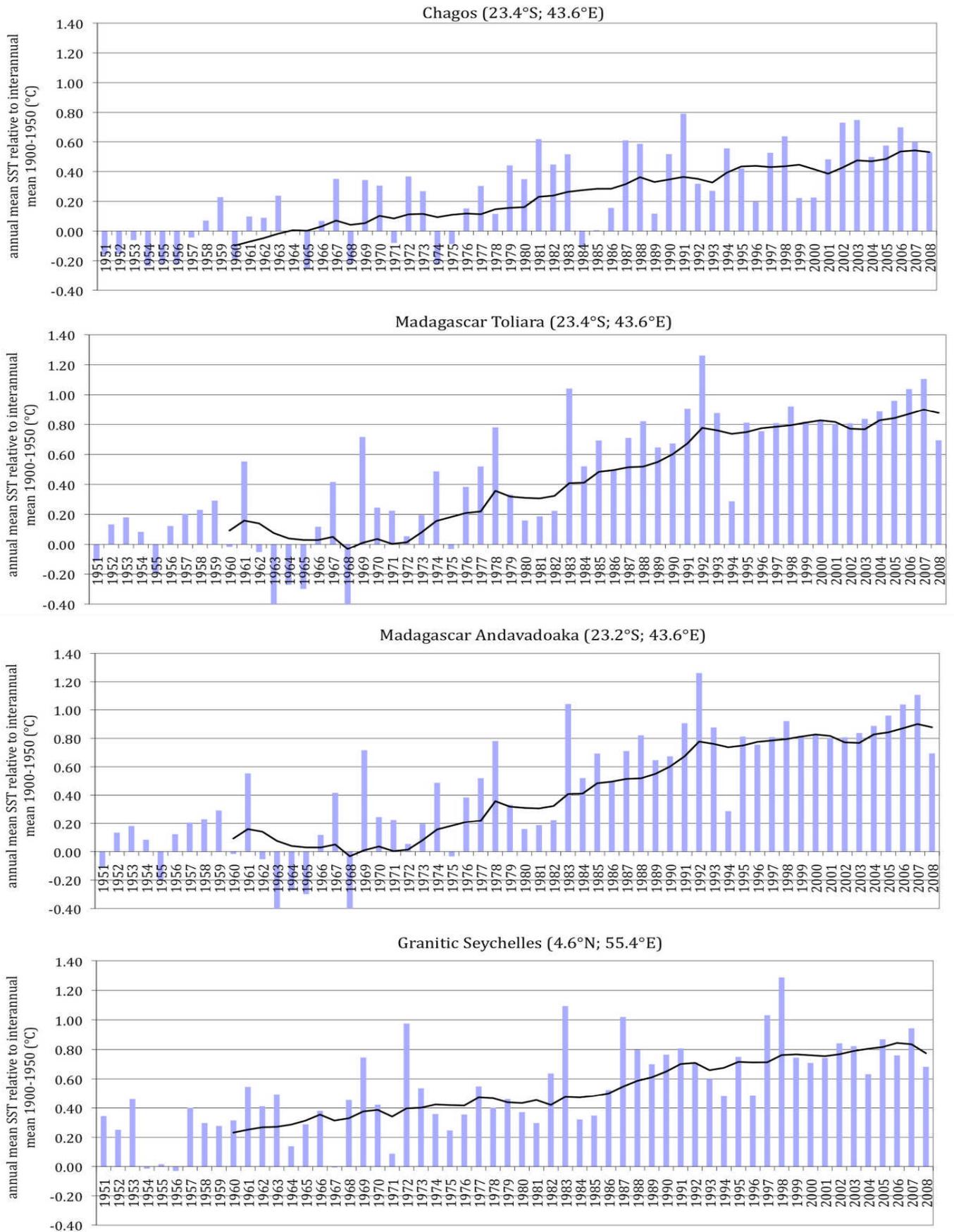


Figure 81a. Mean annual SST deviation from 1900-1950 inter-annual mean; all survey regions, 1951-2008. Black line is 10-year moving average

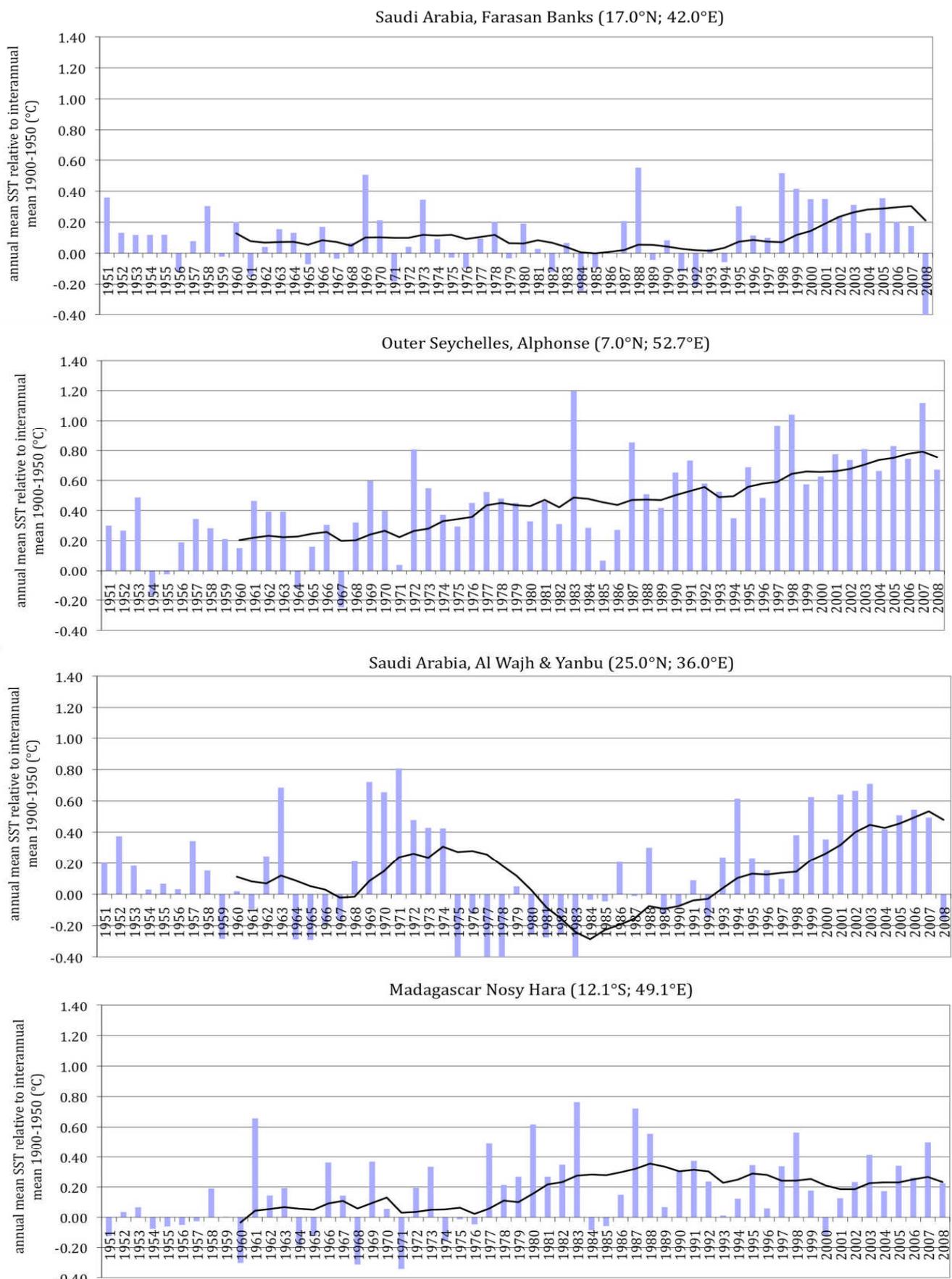


Figure 81b. Mean annual SST deviation from 1900-1950 inter-annual mean; all survey regions, 1951-2008. Black line is 10-year moving average

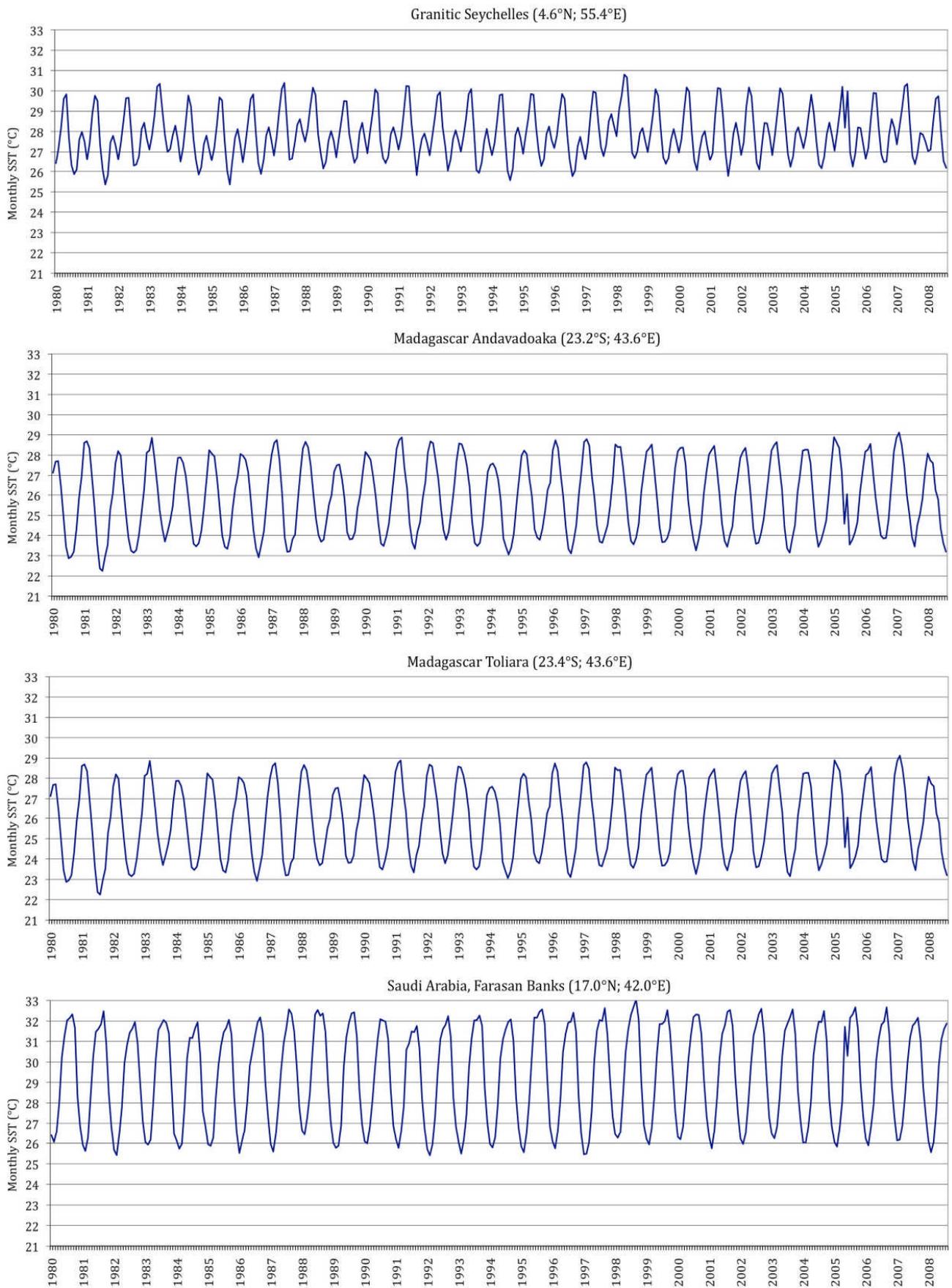


Figure 82a. Monthly SST from 1980 to present; all survey regions

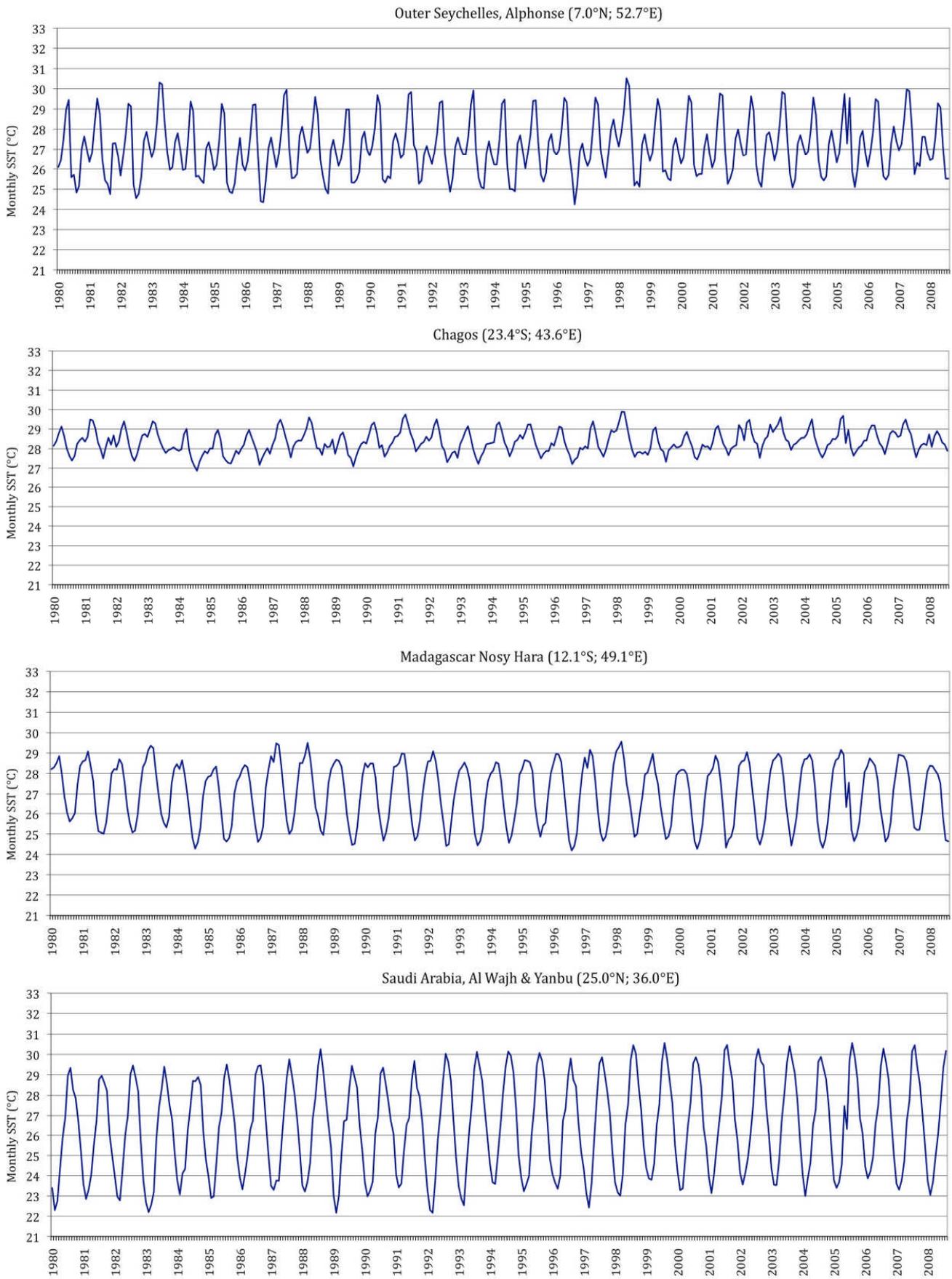


Figure 82b - monthly SST from 1980 to present; all survey regions

DISCUSSION

10 Key findings

Coral communities show considerable spatial heterogeneity at local and regional scales. Communities differ between and within regions based on all variables assessed; taxonomic richness, taxonomic equitability and dominance, coral size frequency distribution, colony abundance per unit area, colony surface area per unit area, and the size distributions of individual taxa.

A number of conclusions may be drawn:

10.1 Coral size frequency distributions

- (i) Relative dominance of any given taxon and/or colony size class normally differs markedly within a coral community depending on whether measured in terms of numerical abundance or surface area of colonies. Characterisation of the taxonomic or size composition of a coral community typically differs based on whether the community is defined in terms of relative numerical abundance or relative surface area dominance of colonies; different variables can lead to profoundly different interpretations of coral communities.
- (ii) Coral communities have positively (right) skewed size frequency distributions when frequency is based on colony abundance data, and more negatively skewed distributions when based on surface area data. Communities are numerically dominated by the smallest cohorts, with colony survivorship increasing with size, and with considerable differences between taxa. Hard coral survivorship is governed by size-dependent mortality rates that vary between genera. These observations are typical of a type-3 survivorship curve, whereby susceptibility to most mortality agents decreases with increasing colony size (Hall and Hughes 1996)(section 7.1 and 7.2; pages 94 and 106 respectively).

- (iii) The relationship between colony abundance and colony surface area per coral size class is distinctly non linear as emphasised by the very large contribution to total coral surface area made by a relatively very small number of the largest colonies, at all regions (section 7.1; page 94).

10.2 Juvenile abundance and recruitment

- (iv) Visual-light surveys under-detect the smallest cohorts, as evidenced by the increasing size frequency distributions of juvenile corals between 1-3 cm in size across all regions using visual-light surveys; a trend contrary to coral population theory.
- (v) Ultra-violet census leads to a demographic 'correction' of the size frequency distribution curve (section 8.1; page 169). The severity of under-detection of colonies using visual light increases with decreasing colony size.
- (vi) Within reef regions, juvenile colony density is generally higher at sites where there is a greater availability of unoccupied hard substrate suitable for coral settlement. Conversely, a higher abundance of competing benthic groups results in lower juvenile colony abundance. Sites with larger areas of substratum available for settlement show increased abundance of juveniles at all sizes - including newly-settled recruits 1-2 cm in diameter – thus the higher levels of juvenile abundance seen are a result of increased recruitment, not merely higher juvenile survivorship.
- (vii) Coral density (numerical abundance of colonies per unit area) shows extremely high variability between reefs and regions (this study showed up to 470-fold differences in juvenile colony density and up to 75-fold differences in adult colony density between sites)(section 7.1.1; page 94).
- (viii) The relative composition of adult corals bears little relationship to that of juvenile corals. Juvenile corals cannot be used as a predictor of adult coral assemblages (nor *vice-versa*) and differential taxonomic dominance

between juvenile and adult cohorts should not be assumed to infer instability within a community.

10.3 Inferring reef complexity

- (ix) Conventional measures of benthic 'coral cover' provide a poor indication of total coral surface area within a reef, typically underestimating the total coral surface area of a reef by at least 50%. Measurement of actual coral surface area provides a more variable and sensitive measure of coral cover.
- (x) Measures of total coral surface area, expressed as a ratio relative to the 2-dimensional surface of the sampled area, are strongly related to the coral-built structural complexity of a reef, and provide a quantitative measure of reef rugosity.

10.4 Sensitivity of coral community surveys relative to benthic composition

- (xi) The field methods and multivariate analysis approaches used in this research to detect differences in coral communities are capable of discriminating sample groups based on adult or juvenile communities, using colony abundance or surface area data, at family or genus level, and with varying degrees of transformation.
- (xii) These methods are far more revealing than most commonly used conventional benthic assessments such as intercept surveys, cover values and diversity, which rarely capture discriminatory information on overall composition of coral communities, let alone the structure of populations within them.
- (xiii) Comparisons of values of absolute 'coral cover' between reefs may be misleading, failing to detect important size or taxonomic differences between coral communities. Measures of 'cover' of dominant benthic groups across the Farasan Banks failed to detect evidence of severe coral mortality that affected almost half of sites visited.

Conversely, values of coral community composition based on the methods employed in this research showed clear and significant separation of mortality-affected sites.

10.5 Effects of environmental disturbance on coral communities

- (xiv) Environmental stress to coral communities, for example through persistent anthropogenic disturbance and/or bleaching-related mortality, results in reduced colony density (abundance per unit area), as well as altered taxonomic composition, notably reduced taxonomic richness, higher generic dominance, and lower generic equitability (evenness) of coral communities. This applies at both at inter- and intra-regional spatial scales, based on a range of univariate and multivariate analytical approaches.
- (xv) This study indicates some evidence that environmental stress may result in depressed colony size frequency distributions (in both communities and populations), however these findings are inconclusive and require further investigation.
- (xvi) When observed, patterns of dissimilarity in coral communities between sample groups defined *a priori* (for example different geographical regions) are generally consistent for differences in taxonomic composition and size distribution. In other words, communities exhibiting different coral taxonomic composition also show differences in coral size distributions. Thus different taxonomic compositions of coral communities commonly also have distinct size distributions (section 7.5; page 132). Consequently, in the absence of taxonomic data, changes in the size structure of a coral community should not be assumed to indicate a shift to smaller or larger corals – size distribution changes also result from changes in taxonomic composition.
- (xvii) Where observed, significant differences between reef sites based on coral community composition data are consistent whether analysis is carried

out across all genera, or restricted to a smaller subset of taxa. Between-site differences are normally attributable to this subset of discriminating genera. These account for the main differences between reefs in multivariate analyses, and are considered the most 'important' taxa in differentiating ecologically meaningful changes between coral communities. A reduced assemblage of target genera is, however, unable to differentiate samples based on taxonomic data (section 8.2).

- (xviii) *Acropora* is not necessarily the natural dominant taxon on 'healthy' Indian Ocean reefs. Its absence from a coral community should not be assumed to indicate disturbance. However this research provides indications of a higher relative abundance of *Porites*, and lower relative abundance of Acroporidae, at sites affected by mortality in the Farasan Banks, as well as a higher relative abundance of Faviidae at disturbed sites in Madagascar.
- (xix) Temporal analyses are required to understand changes in coral communities over time. The field methods and analytical routines employed in this research provide a framework for future studies of region or site specific temporal trends.

10.6 Inferring reef resilience and recovery potential

- (xx) Measures of coral density, surface area, taxonomic composition and size frequency distribution provide useful parameters for interpreting resilience of coral communities. This research emphasises certain aspects of coral communities considered to favour recovery from mass mortality (such as high levels of recruitment and available hard substratum for settlement), as well as factors inhibiting recovery, such as the presence of competing adult corals inhibiting juvenile settlement.
- (xxi) Enhanced understanding of the composition of coral communities provides new insight into the failure of management efforts to safeguard reefs with low resilience in the Granitic Seychelles, whilst at the same

time highlighting the extent of recovery at well-managed resilient reefs in southern Madagascar and Chagos.

- (xxii) Not all reef systems harbour innate recovery potential: data from the Granitic Seychelles indicate that, even when benefiting from effective management, certain reef systems may have already deteriorated to a stable algal-dominated phase and, unlike the Andavadoaka reefs, are unlikely to retain any ability to recover.

- (xxiii) Assuming repeated exposure of the Indian Ocean's reefs to ongoing bleaching-related mortality episodes, adequate substratum stability is important to the recovery of coral communities. This research provides evidence of the influence of substrate stability in facilitating or impeding reef recovery following mortality.

11 Variation in coral communities at different spatial and temporal scales

This region-wide study of coral community composition and population structure highlights the considerable differences in coral communities that exist both within and between survey regions.

Coral reefs are highly dynamic systems showing enormous natural spatial and temporal variation in communities at a range of scales. Successional, episodic and cyclical changes are normal. Given such patchiness, a steady state coral reef is hard to define. Wide differences in coral communities observed in this research emphasise the importance of carrying out reef monitoring at different spatial scales, since it is important to avoid misinterpretation of normal patterns of ecological heterogeneity. Thus the wide geographic spread of survey regions in this study was chosen to reflect different levels of exposure to past and contemporary environmental stress, while the survey sites within regions were spread to capture within-region ecological heterogeneity as accurately as possible.

Impressions of reef health and quality commonly vary according to approximate local 'standards' of reef condition. The depauperate state of the Granitic Seychelles reefs illustrates this point. Without comparative data from other regions, or data from past years, the present low abundance of Granitic Seychelles juvenile corals might not have been apparent. Although past surveys of juvenile coral abundance have recorded similarly depauperate juvenile communities at other exploited reef sites in the Indian Ocean, such values mean little in isolation (Obura 2002). When examined at a larger spatial scale, it is clear that Granitic Seychelles reefs are now both extremely impoverished and have very low juvenile replenishment.

Care is also needed owing to the three-year time scale over which data were collected. Because field surveys only capture a view of a coral community or population at a single point in time, an investigation of spatial is inevitably confounded by temporal variability, such as the different lengths of time following the important 1998 event, and possibly different spawning frequencies.

11.1 Farasan Banks, Saudi Arabia

The Farasan Banks differed markedly from other reef regions, showing higher colony density and colony surface area for both juvenile and adult corals than any other reef region surveyed in this study. The region also showed the lowest between-site variability in adult colony density, despite clear coral mortality at almost half the sites surveyed. Colony density and surface area values were also higher for juvenile colonies than at all other comparative CCCR survey regions, although notably lower than the Al Wajh (Saudi Arabia) survey region for adult colonies (however it is possible that the latter may be a result of differences in sampling techniques for juvenile colonies, discussed in section 14.5.1; page 227).

Farasan Banks reefs also showed consistently higher genus and family-level taxonomic richness than sites in other survey regions. Despite high diversity, the region had the lowest taxonomic equitability of all regions visited, emphasised by the high levels of generic dominance of *Porites*. No other reef

region for which comparable juvenile coral data are currently available shows similar absolute or relative levels of dominance of *Porites* or Poritidae.

The high abundance and surface area of colonies at reefs in this region contributed to the extremely high structural complexity of the reefs, mainly due to *Porites* colonies. Approximately one quarter of sites showed values of total colony surface area greater than 100% of the 2-dimensional transect area.

At a number of sites the benthic community was so heavily dominated by live adult corals that juvenile colony abundance was depressed relative to less coral-dominated sites, however coral recruitment was still exceptionally high.

Recruitment is therefore not a limiting factor to the recovery of Farasan Banks reefs. Indeed, unlike the adult coral communities, multivariate analysis of juvenile coral communities showed no significant differences in size frequency distribution or taxonomic composition between mortality-affected and unaffected sites within the Farasan Banks.

Moreover, there was negligible algal overgrowth on the region's abundant dead coral surfaces, which suggests that competition for benthic space from algae is not a factor prohibiting coral recovery, and that phase shifts to algal-dominated conditions are not posing a threat to the ecological stability of Farasan Banks reefs. The low levels of algal growth may contribute to the high levels of coral recruitment observed. Algal growth is likely to be inhibited in the region by high levels of herbivory, which may be maintained by existing low levels of fishing effort, as well as by the nutrient-poor oligotrophic conditions of most outer reefs (Devantier et al. 2000).

Despite an extremely high colony abundance and architectural complexity, coral communities in the Farasan Banks had a lower upper size limit and significantly depressed size frequency distribution relative to all other survey regions except the extremely degraded Toliara region. The region showed lower average surface area of colonies >1.6 m than all other survey regions in both this study

and comparative CCCR regions (with the exception of Toliara), and was the only region from which no corals were recorded in the largest size category (>3.2 m maximum diameter).

11.1.1 Probable cause of coral mortality in the Farasan Banks, Saudi Arabia

It is unclear why there is a relative lack of large old colonies in the Farasan Banks, even when compared to other, otherwise more degraded and depauperate regions such as Granitic Seychelles. A low number of large colonies within a coral community is generally considered to be indicative of past mortality (Obura 2009).

The observations of unusually small corals at the Farasan Banks are based on values derived from all sites in the region, so if reef mortality is the driver of the observed depressed size structure of Farasan Banks coral communities, it may be hypothesised that mortality has affected all sites in the region at some point in the recent past – not only those on which recent mortality was actually observed. Given the lack of past monitoring and historical data from Farasan Banks reefs, it is quite possible that mortality events such as those observed at affected sites have occurred throughout the recent past, affecting either individual reefs in isolation (as observed during this study) or all reefs throughout the region.

Previous documented bleaching in the central Red Sea was most severe in shallow reef environments (DeVantier et al. 2004). The mortality observed at affected sites in this research spanned all colonies at all depths on from the upper reef crest down to the limits of survey visibility, in excess of 60 m, where thermal stress and/or UV irradiation are likely to be much less severe. Mass bleaching at other Indian Ocean reef sites exposed to similar oligotrophic conditions has typically only occurred down to a clear transition depth, usually a thermocline at 10 – 15 m depth below which bleaching was much less (Sheppard and Obura 2004). The latter were attributed to persistent thermoclines supporting warm shallow water. Clearly therefore, either the bathymetry of the southern Red Sea precluded the development of thermoclines in this region,

leading to a greater depth of warmed water, or the observed mortality was not the result of an anomalous heating event.

An alternative cause of the coral mortality may be predation by the coralivorous *Acanthaster planci*, consistent with outbreaks of dense aggregations of the starfish at other areas of the southern Red Sea (Ormond and Campbell 1974). Daytime predation on *Porites* at 'unaffected' sites was seen throughout the Farasan Banks (despite *Porites* not being a favoured prey of *A. planci* (Berumen and Pratchett 2006)), in marked contrast to the absence or comparatively very low levels of starfish observed at sites affected by heavy mortality in this region. The 'plague' nature of *A. planci* infestations is such that populations are likely to quickly disappear from a predated reef once no living corals remain. The species' 'boom and bust' life history dynamics indicate that, if this predator were responsible for observed coral mortality here, recovery should be viewed in the context of repeated setbacks rather than being progressive or as a smooth succession.

As well as having by far the highest mean annual sea surface temperature (SST) of all the regions studied in this research, the Farasan Banks region also has the highest intra-annual seasonality (amplitude, Figure 82; page 182) and intra-annual standard deviations in SST (Figure 80; page 179). Studies of East African reefs following the 1998 bleaching event showed that coral mortality between regions decreased with increasing SST variability (McClanahan et al. 2009), which is consistent with SST data from regions in this study, where the highest documented incidences of bleaching-related coral mortality occurred where the annual temperature variability was lowest (Figure 82; page 182); namely the Granitic Seychelles and Chagos.

If the hypothesis that increasing intra-annual temperature variability reduces a region's susceptibility to bleaching is correct, the Farasan Banks are less likely to have experienced bleaching-related mortality than other regions studied. Moreover, this region shows consistently smaller (less positive) SST anomalies in annual mean values relative to the 1900-1950 inter-annual mean than all other

regions, indicating a weaker warming trend than all other survey regions over the past century.

It has also been hypothesised that the oceanographic character of parts of the Red Sea, which creates large zones of upwelling, may offer the region some protection against mass bleaching episodes (Devantier et al. 2000). Devantier (2000) suggests that coral communities in upwelling areas are likely to be important in the maintenance of coral populations and conservation of biodiversity, and act as source populations for replenishment of areas affected by bleaching and other disturbances. Empirical data from both the Atlantic and Indian Oceans suggest a link between such areas of cool water upwelling and enhanced coral recovery after bleaching (Reigl and Piller 2003).

The coral-dominated present-day condition of many of the Farasan Banks reefs suggest that the region's corals may have adapted to very high annual mean water temperatures by developing a higher thermal tolerance threshold, with the duration of any bleaching stress limited by the region's very high intra-annual temperature variability, and relatively weak long-term inter-annual warming trends.

Thus it is unclear whether the observed mortality in the recent past here is due to *A. planci* predation or to coral bleaching. However regardless of its cause, the observations of smaller colony size and extremely high juvenile abundance at the Farasan Banks indicate that although mortality episodes have occurred in the recent past recruitment is presently substantial.

11.2 Granitic Seychelles

The Granitic Seychelles was the most depauperate region surveyed, with the lowest density and surface area of both adult and juvenile corals. They were also more impoverished in terms of colony abundance than all comparative CCCR regions, with the exception of the adult coral community at Nosy Hara, Northwest Madagascar, which was similar in terms of colony density and surface area. Taxonomic richness was also markedly lower than all regions except the

highly degraded Toliara Madagascar region. Generic dominance was higher than both Madagascar survey regions due to the prevalence of Poritidae and Faviidae at many sites. However, Granitic Seychelles reefs did show but a higher equitability of genera than the Farasan Banks region.

A number of formerly recorded genera were absent from surveys carried out in this study. These were *Seriatopora*, *Pachyseris*, *Echinophyllia* and *Oxypora* (one colony of *Pachyseris* was recorded at St Anne Island, Mahe). These may be among the first taxa to have been extirpated from the region's reefs as a result of failed reef recovery.

Granitic Seychelles reefs have clearly shown very poor recovery since 1998. Many sites are in an advanced erosional state with little available hard substratum suitable for coral settlement. The few non-granitic rocky sites are mostly colonised by profuse turf and macroalgal growth, preventing effective settlement and/or survival of coral larvae. A number of sites known to have previously shown thriving reef growth (Jennings 1996) no longer appear to be actively accreting. Reef complexity was also very low at most sites, with only one site showing total coral colony surface area above 80% of the total 2-dimensional transect surface area. This condition is consistent with earlier observations of the loss of reef complexity at the same sites in 2005, considered to be a result of bioerosion and subsequent collapse of dead reef frameworks (Graham et al. 2006).

With the exception of corals growing on granite, there is no indication that Granitic Seychelles coral communities have shown appreciable recovery over the 3 years since the latter study, or indeed since the mass coral mortality episode 10 years prior to this study. On the contrary, on carbonate and sandy substrata, the pervasive structural collapse and phase shift of Granitic Seychelles reefs towards low diversity macro algal-dominated states has continued, indicating very low recovery probability.

Median colony size at this region (in terms of contribution to cumulative colony surface area) in apparent contrast, was almost double that observed in the Farasan Banks, with larger, probably older colonies contributing disproportionately to the overall surface area of corals. This indicates survival of some very large colonies as well as low recruitment. Multivariate analyses across all sites and size classes showed significantly larger size frequency distributions of colonies in the Granitic Seychelles compared to the Farasan Banks. This difference is not attributable to the reef sites located on hard granitic substrata, which generally showed far higher colony abundance and surface area; indeed, on the contrary, the granitic sites showed lower mean colony sizes than the more depauperate non-granitic reef sites.

The largest colonies were of Poritidae and Faviidae; generally slow growing taxa, which, given their sizes, are likely to be survivors of the 1998 and subsequent bleaching-related mortality episodes. Such large colonies would usually suggest high levels of fecundity. Coupled with the presence of diverse coral-dominated reefs based on granitic substrata throughout the region, the presence of these large fecund thermally tolerant colonies would be expected to indicate viable local sources of coral larvae within the Granitic Seychelles. Moreover, the correlation between juvenile colony abundance and available hard 'settlement' substratum suggests that, at many sites in this region, corals are successfully recolonising unoccupied substrata. However, given the generally very low numbers of juvenile colonies even when colony detection was supported by the use of UV, it might be reasoned that low levels of coral settlement – and/or post-settlement survival are limiting reef recovery in the region.

It is unclear whether recruitment failure is due to adult colony reproductive failure, or to failed larval settlement caused by the dominance of competing macro-and turf-algae on many reefs, or to post-settlement mortality of coral spat due to predation or overgrowth from competition with faster-growing algae. Decreased settlers may indicate a reduction in fertile colonies, a feature that might be expected after a high stress or mortality episode. Equally however, the prolific abrasive loose coral rubble typical of many reef sites in this region may

also be a cause of juvenile colony mortality, as a result of overturning of rubble pieces during storms and consequent abrasion of highly vulnerable newly-settled spat. This phenomenon of substrate mobility is also hypothesised to be a cause of recruitment failure and inhibited reef recovery at certain reef sites in Madagascar where the dominant pre-mortality coral species has disintegrated following mortality resulting in a remnant unsecured coral debris, persisting for over 10 years (section 11.3; page 199). Studies of settlement dynamics and colony survivorship on natural and artificial substrata in this region would be required to test these hypotheses.

Regardless of its cause however, recruitment failure is undoubtedly severely limiting the recovery of many Granitic island Seychelles reefs. The longer such recruitment failure persists, the more fragmented the underlying substratum will become as a result of mechanical and biological erosion, in turn becoming increasingly unfavourable to coral settlement. The results of this research indicate that coral reefs located on carbonate and sandy substrata within the Granitic Seychelles have passed the threshold of viable recovery, now being in a self-reinforcing, non-coral dominated phase. Given also the erosion and disappearance of large areas of remaining dead coral framework on reefs located on carbonate and sand substrata, recovery of non-granite substratum Granitic Seychelles reefs now seems extremely unlikely.

Clearly, management efforts have failed to have any impact on juvenile or adult coral recovery either, in particular in protected sites relative to unprotected reefs. This observation lends further support to regional observations of the failure of existing Indian Ocean reef management efforts to promote ecosystem recovery following large-scale disturbance in the region. In part this is likely to be due to the fact that protected areas commonly are focussed on reefs once characterised by prolific growth of thermally intolerant and/or branching coral taxa, which have generally shown the highest declines in coral cover following disturbance events (Graham et al. 2008).

This research indicates that existing marine protected areas in the Granitic Seychelles, although generally effectively enforced, are not zoned to protect reefs with any likely recovery potential. For example, protected sites at Cousin Island recorded amongst the lowest values of coral abundance, surface area and diversity of all sites in all regions surveyed, with mean generic richness of the three protected sites at Cousin Island being less than half that at other sites (8.3 ± 1.5 SE compared to 18.8 ± 1.3 SE).

Given the possibly decreasing production of locally-derived recruitment originating within the Granitic Seychelles, safeguarding the remaining viable recruiting coral communities of the region – many of which are characterised by structurally fragile and thermally intolerant habitat-forming taxa such as *Acropora clathrata* and *A. abrotanoides* - should be an urgent priority. Currently, none of these priority sites are protected within fisheries no-take zones in the Granitic Seychelles.

Any management recommendation drawn from these findings should emphasise the critical importance of protection of remaining granitic reefs, since these sites offer greater substrate stability than carbonate reefs, and show more effective survivorship of coral recruits post-settlement. Assuming that the observed collapse, erosion and failed recruitment of reefs on non-granitic substrata is broadly representative of reef condition throughout the broader shallow Seychelles Bank (where climatic and anthropogenic stresses since 1998 have been similar), the few small, granite-based coral communities within the Seychelles Bank will play an increasingly crucial role at a regional level as refugia for remaining coral populations.

These observations of cascading deterioration of Granitic Seychelles reefs are not unique in the central Indian Ocean. In the Maldives too, slow and scattered formation of new reef substrate has been outweighed by the collapse of large dead colonies, with reefs being converted to levelled fields of rubble, only partially consolidated by encrusting corals (Schuhmacher et al. 2005).

Importantly, these results provide a new reference against which to assess future changes and dynamics within Granitic Seychelles coral communities, notably a quantitative site-specific measure of the scarcity of coral recruits and the depleted populations of adult corals at most reef sites.

11.3 Madagascar Andavadoaka

Andavadoaka's reefs showed moderate levels of colony density and surface area, with the highest levels of inter-site variability in adult density of all regions studied. The region showed the second highest level of taxonomic richness of adult corals, and low taxonomic dominance across all survey sites as a result of high generic evenness.

Andavadoaka was the only region whose reefs were dominated (in terms of numerical abundance of colonies) by Acroporidae. The region's reefs also showed a higher average surface area of colonies in the two highest size categories (>1.6m) than all other survey regions in this study and comparative CCCR regions, with the exception of Al Wajh, Saudi Arabia. The large colonies accounting for these values have mostly settled within the last 8 years, namely after the last mass mortality episode thought to have affected the region (Harding et al. 2006).

Within protected reefs coral cover approached 80%, showing a far higher relative abundance of structurally complex genera than unprotected sites, with approximately 15-40% of colonies belonging to the fast-growing and architecturally complex Acroporidae and Pocilloporidae. The proportion of corals belonging to structurally complex taxa was consistently highest at sites with the greatest total cover of hard coral. This observation is consistent with meta-analyses of responses of coral cover from sites throughout the Indian Ocean between mid 1990s and 2005, which have shown spatially variable responses but a strong correlation between loss in coral cover and loss of structural complexity (Graham et al. 2008). It is clear that most of Andavadoaka's reefs have likewise suffered a reduction in their three-dimensional architectural framework.

The region's reefs are chronically disturbed by fishing pressure, with far higher fishing effort than in the Granitic Seychelles or Farasan Banks (Blue Ventures, unpublished data). A notable exception are the reefs protected from fishing within the Velondriake Locally-Managed Marine Area (LMMA), where fishing is currently prohibited and management effectively enforced by communities. The LMMA had been enforced for less than one year at the time of surveying, however the sites benefited from a degree of *de facto* protection prior to implementation of the protected area. The highest fish biomass and diversity values in the region have been recorded at these sites, which have traditionally experienced relatively low levels of fishing intensity as determined by fisheries landings data (Blue Ventures, unpublished data). Coral cover and complexity within these protected sites has recovered to current high levels from a very degraded state in 2004 (Blue Ventures, unpublished data), indicating a high level of innate ecological resilience of the region's reefs.

It has been repeatedly shown that even where warming is causing reef deterioration, recovery can be rapid where there are minimal direct anthropogenic stresses, but recovery may not occur at all where there is also pollution and over-fishing (Harris and Sheppard 2008; Sheppard et al. 2008; Hagan et al. 2008). Data from this region provide a compelling case that recovery of Andavadoaka's unprotected reefs may currently be inhibited by high levels of fishing effort. Appropriate management to increase herbivory will be essential to reducing erect algal abundance and promote reef recovery in the region (McClanahan et al. 2009).

Recent research carried out elsewhere in southwest Madagascar has described the broader southwest region as a marginal reef region having low generic diversity, unlikely to provide refuge for coral diversity during ocean warming, and showing no evidence of existing coral refugia (McClanahan et al. 2009). However, the present work demonstrates high taxonomic richness and substantial ecological resilience of coral reefs.

It is likely that the low diversity conclusions of McClanahan (2009) are a sampling artefact, since sampling was largely restricted to heavily degraded lagoonal sites, all at a shallow depth of < 3m. The chronic fishing pressure experienced throughout the region, and the region's very large tidal regime (averaging 3.2 m making reefs up to 6 m depth easily accessible to gleaners and skin divers), are such that all shallow reefs are on the whole very disturbed, and not considered representative of deeper reef communities.

Southwest Madagascar's reefs showed the lowest mean SSTs, high inter-annual variability and the highest intra-annual variability of all regions except those in the Red Sea (Toliara and Andavadoaka being effectively identical in terms of SSTs relative to other regions). Whilst these characteristics suggest low susceptibility to bleaching (McClanahan et al. 2009), the region also shows the highest rise in mean annual temperature relative to the 1900-1950 inter-annual mean, a factor that may indicate higher vulnerability to future warming. At a national level, the region's coastal waters are experiencing faster rises in SST than elsewhere in the country, approximately $0.016^{\circ}\text{C yr}^{-1}$; roughly 3 times faster than northern reefs, and significantly above global and East African average rates of sea surface temperature rise (McClanahan et al. 2009).

11.4 Madagascar Toliara

Sampling on the *Grand Récif* was low compared with other regions. Toliara's reefs showed the lowest taxonomic richness of all regions surveyed, but had low generic dominance and the highest generic evenness. The region was very low in architecturally-complex coral genera, with only 15% and 7% of colonies recorded (by abundance) belonging to the families Acroporidae and Pocilloporidae, and the two most dominant genera recorded being *Echinopora* and *Porites*. Corals showed a truncated size frequency distributions, with no corals >1 m maximum diameter (Harris et al. 2010).

Causes of mortality in the *Grand Récif* may be a combination of ocean warming, which is considered to have caused mass bleaching in this region three times between 1998 and 2002 (Harding et al. 2006; McClanahan et al. 2009), as well as

severe over-exploitation and pollution of the reef. Fish diversity and biomass on the *Grand Récif* are extremely low, a result of present high levels of fishing (Harris et al. 2010). The rapid rise of discharged, untreated sewage from the growing city is also likely to be important. This condition contrasts markedly with the much better coral cover seen in less exploited protected areas in the Andavadoaka region, where SST levels have been similar but which do not have significant sewage discharge or such high fishing intensity.

Despite the heavily degraded condition of Toliara's reefs, the hard benthic substratum and persisting coral communities indicate that recovery of the *Grand Récif* may still be viable, providing local stressors can be adequately mitigated. Observations of reef recovery from equally degraded conditions elsewhere in Madagascar's southwest reef system (Blue Ventures, unpublished data) provide an indication of the potential for reef recovery in the face of effective management.

11.5 Chagos

Data describing the generic and size frequency composition of adult coral communities were not collected from the Chagos archipelago. However, based on benthic composition and juvenile coral data, the results of surveys carried out in this study and subsequently show that many Chagos reefs have recovered to benthic cover values similar to those of 30 years ago (Sheppard 1980) with substantial recruitment, indicating a resilient system with unusually high recovery potential. Moreover, high levels of recruitment of *Acropora* spp. occur and Chagos is regaining its original dominant shallow water coverage of *A. palifera* (Harris and Sheppard 2008; Sheppard et al. 2009; Sheppard et al. 2008; Sheppard 2010, pers. comm.).

The ability of Chagos reefs to 'bounce back' to rich reef communities after experiencing severe bleaching-related mortality has been recorded in few other reef environments in the Indian Ocean, and shows that Chagos reefs have followed a different trajectory to many other reef communities in the central Indian Ocean.

The high resilience and re-seeding capacity of Chagos reef ecosystems may be a result of their undisturbed nature, their complex large deep lagoons, and the archipelago's proximity to the south equatorial current, down-stream from southeast Asian archipelagos. Regular plunges of water temperature of 5-7°C, lasting 1-4 days, have also been recorded on seaward reef slopes in the Chagos archipelago, overlapping with the period of maximum ocean temperatures. Observed fluctuations increased with depth and were not detected by remotely-sensed SST sensors, highlighting the potential role of previously unidentified sub-surface internal waves and hydrodynamic regimes in mitigating the effects of thermal stress at certain 'refuge' reef habitats (Sheppard 2009).

Nevertheless, HADISST SST analyses show that, after the Farasan Banks, Chagos experiences the second highest annual mean SST of all regions surveyed (with Granitic Seychelles experiencing the third highest). Moreover, unlike the Farasan Banks, Chagos and the Granitic Seychelles showed the lowest intra-annual variability in SST of all regions surveyed, as well as a marked trend of increasing annual mean SST relative to the 1900-1950 inter-annual mean. Thus despite its evident strong ecological resilience, Chagos, like the Granitic Seychelles, may be more vulnerable to future thermal stress episodes than other regions surveyed exposed to greater intra-annual temperature variability.

In the aftermath of the 1998 mortality episode Sheppard (2006) noted that members of the genus *Montipora* - commonly smaller and more encrusting members of the Acroporidae in this location than most *Acropora* survived better than *Acropora* (Sheppard 2006). This conclusion was not supported by observations during this study, where *Montipora* - a genus documented to have a high bleaching response (McClanahan et al. 2007) - was extremely uncommon at all reef sites. It is possible therefore that this genus suffered significant disturbance in the 2 years prior to this study.

One additional striking absence was of the faviid *Diploastrea heliophora*. Once noted as common in Chagos (Sheppard, 2006, pers. comm.) this massive Faviid, typically characterised by very large colonies at a range of reef depths especially

in lagoons, was entirely absent in all surveys undertaken in this research. It is possible that this mono-specific genus may now be locally extinct. It is not clear what the ecological consequences of the loss of *Diploastrea heliopora* may be, however this study shows that the species can be a dominant spatial component of reef ecosystems (contributing over one third of adult coral surface area at some reef sites in Andavadoaka, Madagascar).

Relative juvenile colony abundance data can be compared to values obtained from the archipelago in 2001 (Wilson 2007)(Figure 83; page Figure 83). Data from this study are adjusted to remove all juvenile colonies >5 cm, and only data from Wilson (2007) from 7.5 m - 12.5 m depth were used to ensure standardisation of depth sampling. The two studies show very different juvenile coral communities. Five years after the 2001 studies, relative abundance of Agariciids, Poritids and Pocilloporids had all more than doubled, and relative abundance of siderastreids had tripled. Conversely, relative acroporid abundance decreased by over two thirds, from 55% to 18% of juvenile colonies. This was a result of a reduction of *Montipora* colonies from 21% to 2% of juveniles, and of *Acropora* colonies from 34 % to 15% of juveniles.

The 2001 data were collected when Chagos coral communities had shown little recovery, with few adult corals remaining. The area of unoccupied dead coral substrate suitable for juvenile coral settlement was much higher in 2001 than 2006. It is not possible to compare absolute abundances of juvenile colonies between the two studies because of different sampling approaches, but the differences in relative abundance of taxa illustrated in Figure 83 may be a result of successional changes in the juvenile coral community as adult coral cover was restored and settlement space decreased across the archipelago.

For example, the dominant juvenile taxa in 2001 may be more representative of a pioneer community, whereas the 2006 community is likely to have been representative of a more stable community, perhaps favouring genera with greater tolerance of shading from adult *Acropora* colonies.

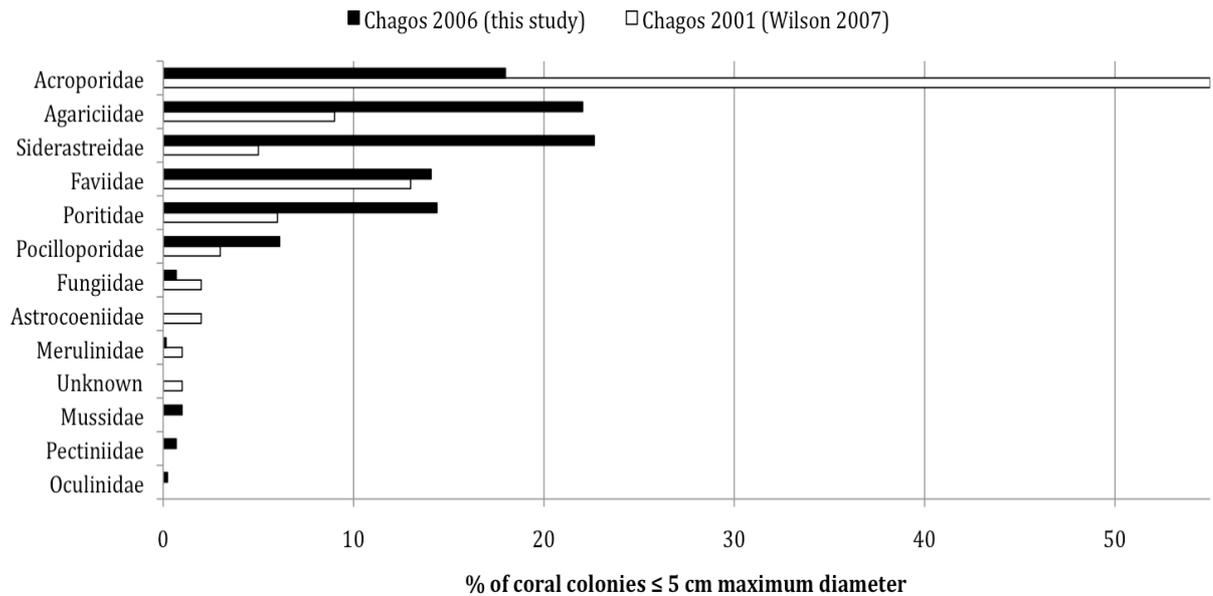


Figure 83. Differences in relative abundance of juvenile colonies (≤ 5 cm maximum diameter) and values obtained by Wilson (2007)

12 Impacts of disturbance on coral community taxonomic and size composition

Coral mortality at almost half of the reef sites within the Farasan Banks survey region allows interpretation of the impacts of recent environmental disturbance on coral communities at a local scale (see section 11.1.1; page 192). At inter-regional scales, the Granitic Seychelles and Andavadoaka, Madagascar provide insight into the possible differential responses of coral communities exposed to different degrees of anthropogenic disturbance, showing different levels of observed ecological resilience in the aftermath of past mass mortality events.

12.1 Impacts on colony size frequency distribution

12.1.1 Impacts on communities

Stable environmental conditions in macro-benthic communities are generally considered to favour K-selected species (Parry 1981). These are characterised by large sizes and long life spans, rarely numerically dominant, but commonly dominant in terms of biomass (or surface area). Disturbance is often hypothesised to favour opportunistic species (*r*-strategists) over K-strategists, resulting in increased relative survivorship of smaller, short-lived *r*-strategists

(Clarke and Warwick 2001). Thus the distribution of numbers of individuals among taxa may respond differently during a recovery phase.

Across all sites studied within the Farasan Banks, disturbed reefs showed fewer large colonies and more abundant small colonies, as well as significantly lower mean adult colony sizes.

In Toliara – the most chronically anthropogenically disturbed region studied – coral communities showed the most truncated size distributions, with maximum colony sizes less than 1/3 of the Farasan Banks – which itself is a region with notably depressed colony size distributions. Colony growth in the region's reefs appears to be constrained by the highly anthropogenically disturbed conditions.

At first sight, data from the Granitic Seychelles do not appear to corroborate with this conclusion: reef sites on granitic substrata, considered to be the 'healthiest' of all reefs surveyed in the Granitic Seychelles, showed smaller colony sizes than sites on carbonate and sand substrata, which are considered to be much more disturbed (section 11.2; page 194).

However this may be explained by the very low levels of recruitment and juvenile colony abundance recorded at non-granitic sites in the Seychelles; the absence of small colonies at these degraded sites, which show recruitment failure, would shift the peak of the size frequency distribution of colonies in favour of the already-established larger enduring survivors. These observations agree with the prediction by Bak and Meesters (1999) that impacted coral assemblages might still contain good numbers of large colonies but would contain reduced numbers of small colonies (Bak and Meesters 1999).

Caution must be taken when interpreting demographic data based on pooled taxa within a coral community. Observed differences in size distribution parameters between reefs may indeed be influenced by differences in colony size. However, given the wide variation in normal colony size distributions between genera, variations in taxonomic composition of coral communities

within and between regions are likely to play a greater role in structuring community size distributions. Inconclusive observations of the effect of disturbance on coral size distributions indicates that investigations seeking to examine whether disturbance favours smaller or larger colonies within communities are overly simplistic.

Testing of this hypothesis must take into account factors such as the taxonomic makeup and dominance of a community, recruitment failure and absolute colony abundance, as well as changes in populations of other taxa, which may influence results and lead to potentially misleading conclusions.

12.1.2 Impacts on populations

Results show significant differences in size distributions between regions for 15 genera, including important structural taxa *Pocillopora*, *Acropora*, *Favia*, *Porites* and *Echinopora*. Whilst increasing disturbance decreases colony sizes, there is no noticeable trend of changing size distributions of these 15 genera between regions (Figure 35; page 123). Clearly therefore, observed differences in community demographic parameters between regions (section 7.5.1.1; page 132) are not driven by consistent population responses across taxa, but are more strongly influenced by differences in the broader taxonomic composition of communities between regions.

Interpretation of differences in generic size distributions between regions is further compounded by differences in the species composition of genera. For example, a change in the locally dominant genus of *Acropora* from *A. humilis* to *A. cytherea*, or of *Pocillopora* from *P. damicornis* to *P. eydouxi*, would result in a substantial increase in the size distribution of the resulting genus population. Thus disturbance cannot be inferred from genus-specific differences in population demography between regions, because of the broad taxonomic differences occurring within genera at large spatial scales. Analysis of generic responses to disturbance therefore focuses on within-region differences in demographic parameters, where differences are less likely to be influenced by natural variation in species diversity and morphological plasticity within genera.

Limiting the analysis to genera within Farasan Banks shows far greater consistency of generic colony size responses to disturbance. With only one exception, where statistically significant differences occur in genus-specific colony sizes between mortality affected and unaffected reefs, colonies are consistently smaller at mortality-affected sites (Figure 36; page 124).

These conclusions are consistent with research in Kenya that has shown coral mortality to increase the relative abundance of smaller colonies and to reduce the size structure of coral populations (McClanahan et al. 2008). Observations of a negative correlation between mean colony sizes of genus populations and the skewness of population size frequency distributions (based on logarithmically-transformed area data) are consistent with studies that have shown that in larger species, larger colonies become increasingly over-represented (negatively skewed) (Bak and Meesters 1998).

12.2 Impacts on generic diversity

Environmental perturbation is generally considered to decrease taxonomic diversity (H') and evenness (J), resulting in increased taxonomic dominance (λ) (Clarke and Warwick 2001). Reef sites in Andavadoaka, Madagascar, showed higher generic diversity and evenness and lower dominance than sites in the Farasan Banks or Granitic Seychelles. Thus based on these indices, disturbance appears to be lower in Andavadoaka than in the Farasan Banks and Granitic Seychelles, consistent with observations of the most severe disturbance to coral reefs in these regions. Diversity indices from Toliara should be interpreted with caution because of the low sample size from this region, however this region's reefs - affected by the highest levels of chronic disturbance of all reefs surveyed - showed the lowest generic richness of all regions.

Environmental perturbations commonly result in increasing variability (standard deviation) in diversity (H') among samples (Warwick and Clarke 1993). Across all regions surveyed, these results show increasing within region variability coincides with decreasing generic diversity (H') and evenness (J), and increasing dominance (λ).

Thus, if increasing variability in H' reflects environmental stress the survey regions ranked in order of decreasing disturbance would be as follows: Granitic Seychelles; Farasan Banks; Madagascar Andavadoaka.

Consistent with their higher variance in diversity indices across samples, reef sites from the Granitic Seychelles are much more diffusely distributed in ordinations based on colony abundance than those from other survey regions. Despite in some cases having a much larger sample size and generic diversity, the other regions show much lower variability and markedly tighter clustering of samples in 2-dimensional ordination space.

At an intra-regional scale, reefs affected by mortality in the Farasan Banks showed lower generic richness and lower taxonomic equitability than all other sites surveyed. Dominance curves from the Farasan Banks also indicate that mortality decreases the numbers of rare taxa and increases the proportion of common taxa.

In the Granitic Seychelles, long-standing well-enforced protected areas have had no impact on taxonomic richness; indeed protected sites in the Granitic Seychelles showed lower generic richness than unprotected sites. However this lack of agreement between the two regions is likely to be a result by the poor resilience of Seychelles reefs, whose condition management has failed to improve.

These observations support the hypothesis that ecological disturbance reduces taxonomic richness of corals. These findings are significant since, like values of absolute coral cover and colony abundance, the diversity of corals within a reef community is considered to contribute to the conservation and maintenance of reef building and biodiversity (Devantier et al. 2000).

12.3 Differential mortality of genera

Observations of conspicuous absentees from some regions provide strong indication of potential local extinctions (notably *Diploastrea* from Chagos; and *Seriatopora*, *Pachyseris*, *Echinophyllia* and *Oxypora* from the Granitic Seychelles).

A high abundance of Acoporidae has been identified as a factor increasing reef susceptibility to climate impacts (Done et al. 2007). The almost ubiquitous highly-eroded depauperate nature of most reef crests and shallow reef slopes in south-western Madagascar suggests that these habitats were once dominated by vulnerable genera (Harris et al. 2010), especially vast mono-specific fields of *Acropora* (Pichon 1978) which are today almost completely absent (Harris et al. 2010). The documented former predominance of e.g. 'loser' over e.g. 'winner' species in the shallow zones of these reef sites, and the subsequent change in coral communities, may have been driven in part by differential susceptibility to thermal stress.

Conversely, faviid corals are considered to be more resistant to stress and instability than other taxa (Bellwood and Hughes, 2001). This family is commonly well represented at marginal reef sites relative to Acroporids, and may therefore be indicative of stressful conditions (Glassom and Chadwick 2006). The family now dominates many reefs in the Arabian Gulf where *Acropora* has all but disappeared (Sheppard et al. 2009). Faviids dominated juvenile colony communities at the Farasan Banks and both Seychelles regions – all considered to have experienced disturbance in recent years.

While valuable, these long-term qualitative comparisons do not allow quantitative investigations of temporal change, which is essential to interpreting the dynamics of coral communities in response to environmental stress, and to accurately describing the nature of any changes that may be taking place in coral communities. Although this research demonstrates the negative impact of environmental disturbance on coral generic diversity at different spatial scales, the temporal snapshots provided do not greatly improve understanding of successional or recovery processes, or prediction of the long-term impacts of

disturbance on coral community composition, in particular in forecasting likely 'winning' and 'losing' taxa.

Thus caution must be taken when making inferences of reef ecological resilience based on contemporary observations of coral communities. For example, so widespread is the evidence of differential susceptibility of taxa to bleaching stress that observations of high abundance of vulnerable genera are increasingly used to infer implicit resilience or resistance of coral reef ecosystems to climate stress. Such inferences may be highly misleading. For example, recent surveys of reefs in the Nosy Hara archipelago, Northwest Madagascar, showed *Acropora* to be the dominant genus, followed by *Porites*, split equally between branching and massive species. Obura (2009) concludes from this observation that there is no evidence of a shift in community structure away from *Acropora* dominance at this site, so that the region's reefs are maintaining their state and function, as well as a high degree of resilience to climate related threats (Obura 2009).

Such speculations of reef resilience based on contemporary observations of coral assemblages are potentially specious, since it must be recognised that branching Acroporid corals are not always the natural pre-disturbance groups. Moreover, in this case, this conclusion ignores the extremely low absolute values of juvenile and adult coral abundance in this region. Indeed the reefs of Nosy Hara exhibited lower juvenile colony density and surface area values than any region surveyed in this research, and its adult colony density and surface area were approximately equal to the Granitic Seychelles – the most depauperate region surveyed in this study. Thus based on comparative analyses with regions surveyed during this study, the Nosy Hara reefs appear to show very low resilience, and are more depauperate than any other region for which data are currently available, albeit with a relative dominance of *Acropora* within a heavily depleted adult coral community.

Equally, contemporary dominance of non-framework genera such as *Porites* or *Favia* should not be assumed to be indicative of a recent post-disturbance framework shift. Surveys carried out in 1993 at Alphonse atoll, Seychelles,

recorded that Acroporids comprised only 1.8% of the scleractinian community, with Pocilloporids and massive *Porites* constituting 10.8% and 80% respectively. In 1992, *Porites* was also recorded as the dominant genus in surveys on the northern reef-slope of Poivre island, in the Seychelles Amirantes (Land 1994). Similarly, there is no evidence that the present *Porites*-dominated condition of Farasan Banks reefs is not a natural climax coral community for this reef region.

12.4 Differential adult and juvenile community structure

Inter-specific differences in relative patterns of abundance and dominance between juvenile and adult coral communities are the result of differences in life history strategies. These variations include growth rates, mechanisms of recruitment, and rates of post-settlement mortality of juveniles. All these factors play an important role in determining adult population and coral community structure (Bak and Engel 1979; Hughes et al. 1999).

This research supports other studies that show a lack of conformity between adult coral abundance and recruitment, and the relative composition of taxa within large and small colony cohorts (Hughes et al. 1999; Bak and Engel 1979). At no region surveyed in this study was the dominant coral taxon the same for both juveniles and adults communities, either at genus or family level. This observation was also true from all comparative CCCR survey regions, with the exception of the extremely depauperate Northwest Madagascar Nosy Hara region, where *Acropora* dominated both the juvenile and adult communities.

This does not indicate instability within a coral community. For example the observed dominance of the juvenile coral community of Chagos by the r-strategist Agariciid *Pavona varians* is not necessarily symptomatic of a coral life strategy or growth form shift in favour of this species; this was also the most abundant species also in terms of colony number in the 1970s (Sheppard 1980). *Pavona* is the dominant Agariciid genus in the Indo-Pacific, and shows high tolerance to thermal stress (McClanahan et al. 2004). Consequently it has been suggested that the genus may share family-specific adaptations with the Atlantic coral *Agaricia* that enable the genus to outcompete other corals during periods of

environmental stress (McClanahan 2000). It has been hypothesised that in conditions of high fishing effort (reduced predation) *Pavona* is highly susceptible to predation by fish, in particular Scaridae and Balistidae (McClanahan et al. 2005) and high thermal stress may drive dominance of this genus (McClanahan et al. 2008). Alternatively, however, the predominance of *Pavona varians* within the juvenile coral community may simply be a function of its life history strategy, favouring high levels of recruitment and mortality, in turn leading to rapid turnover of juveniles and comparatively little representation of the species within the adult coral community's overall surface area. Given the low contribution of *Pavona* to area cover of adult coral communities in Chagos and elsewhere in the Indian Ocean, and the continued trend of reef recovery towards *Acropora*-dominated reefs recorded subsequently (Sheppard 2010, pers. comm.), this second scenario seems the most likely.

13 Ecological consequences of changes in coral communities

13.1 Changes to reef structural complexity

Reef building corals create the habitat and shelter for most of the flora and fauna associated with coral reefs. The exceptionally high biodiversity of coral reefs is in large part due to their enormous structural complexity. Small changes in coral reef ecosystems can be magnified by non-linear interactions, driving functional phase shifts and structural collapses. Any disturbance that has a disproportionate impact on the dominant group may affect overall reef canopy structure and 3-dimensional complexity. Consequently, changes in coral communities are likely to drive changes in the reef rugosity, which is responsible in large part for the high diversity of fish and invertebrates.

Thus broad-scale changes in coral community structure that result in a reduction of the 3-dimensional structural and topographic complexity of coral reefs will inevitably result in dramatic reductions in the abundance and diversity of associated fish as well as other coral-dependent (both coral dwelling and coralivorous) taxa (Wilson et al. 2006; Pratchett et al. 2008; Jones and Syms 2006; Berumen and Pratchett 2006).

For example, changes in the dominant coral from *Acropora* to *Pocillopora* at Tiahura reef had serious impacts on populations of butterflyfishes (Berumen and Pratchett 2006). Across all sites visited in the Granitic Seychelles, reef fish species richness has been documented to decline with a reduction in reef complexity (Graham et al. 2006). Similarly, very low values of fish diversity and biomass in the Toliara region may be due, in part, to the loss of reef complexity and coral-built habitat in this region relative to its past highly complex *Acropora*-dominated condition (Harris et al. 2010).

Consequently, a permanent shift away from structural and frame-building genera such as *Acropora* and *Pocillopora* towards under-story 'binding' genera such as *Pavona* and *Leptoseris* would not just affect a reef's structural complexity, but would also have profound consequences to the biodiversity, ecological niche diversity, microhabitat availability and ecological functional redundancy of the broader reef ecosystem.

Moreover, a coral community dominated by slow-growing low-relief taxa such as many Faviidae, Poritidae or Agariciidae, would have a significantly lower linear extension rate of than one dominated by faster growing branching over-story species such as *Acropora* and *Pocillopora*. Linear extension rates of the common Acroporid *Acropora hyacinthus* are approximately 10 times higher than *Porites* spp.. In the time a *Porites* colony grows to only a few centimetres in height, *A. hyacinthus* colonies can grow into a closed canopy of up to 1 m diameter, 50 cm high (Done and Potts 1992).

In the event of a reef's conversion to a planar community, smaller under-story species would face higher competition with macro-algae for reef space and light. Further, in the absence of Acroporidae and Pocilloporidae, which are among the fastest growing corals and the preferred diet of predatory *Drupella* and *Acanthaster*, slower growing taxa such as Agariciids might face elevated pressures from predation.

Perhaps most critically, the dynamic relationship between accretion and erosion on a reef environment determines whether a reef is growing or shrinking. A reef dominated by species with slow growth and linear extension rates may be unable to accrete carbonate to keep up with rates of erosion.

Evidence of this exists from regions surveyed in this study, notably in the Granitic Seychelles and Toliara, both of which have lost their former dominance of fast-growing branching corals (Jennings et al. 1996; Pichon 1978; Graham et al. 2006). In Toliara, the reef height has already been lowered by the loss of the once abundant reef flat corals (Harris et al. 2010). The greater distance between the surface of a reef and low water level, sometimes termed 'pseudo sea level rise', is known to considerably reduce the breakwater effect of reefs (Sheppard et al. 2005). Loss of breakwater function can result in increased erosion of shorelines, with potentially severe consequences, in this case for the city of Toliara, which lies on a flat coastal plain only marginally above sea level, relying on protection by the Grand Récif from inundation from storms. Heavy oceanic swells of southern ocean origin and amplitude of 1-3 m are common to Toliara, occurring independently of local weather, with swells of 3-5 m being not exceptional (Pichon 1978). Cyclonic activity is also high in southern and western Madagascar, with severe damage to affected areas occurring on an approximately annually. Additionally, the smoothing of the reef flat is almost as important as the loss in absolute height, because of the reduction of friction when corals are absent (Sheppard et al. 2005). The result may be greater exposure to wave energy on the coast, and heightened coastal erosion.

In geological time, such profound restructuring of coral community composition, as described above, is likely to be a highly exceptional occurrence within a coral community. Studies of cores from lagoonal reefs in both the Belizean rhomboid shoals and the Panamanian Bahía Almirante show 2000-3000 years of relatively undisturbed continuous dominance of stagshorn *Acropora cervicornis* and branching *Porites* spp. (primarily *P. furcata*) respectively (Aronson et al. 2004) (Riegl 2002). Departures from these stable branching coral-dominated states were rare and spatially limited throughout the palaeontological record, until

large-scale perturbations since the late 1980s resulted in convergence of both systems to a historically novel state dominated by the brooding agariciid *Agaricia tenuifolia*. These unprecedented coral replacements, brought about by an outbreak of white-band disease and changes in water quality at the Belizian and Panamanian sites respectively, may therefore be considered the most significant perturbations in several thousand years of the reefs' history (Aronson et al. 2004).

13.2 Implications for management

Differential susceptibility of coral taxa to climate-related disturbances has profound implications to coral reef management, in particular marine reserve design.

Many of the world's marine reserves have been established in areas selected for their rich coral cover – in particular high *Acropora* cover. Meta-analyses of responses of coral cover from sites throughout the Indian Ocean between the mid 1990s and 2005 showed evidence that percentage declines in coral cover were greater within no take areas than outside no take areas, probably on account of the fact that such zones are commonly sited in areas with prolific *Acropora* and had higher cover to start with (Graham et al. 2008). Moreover, recovery rates across the Indian Ocean were no different between No Take Areas (NTAs) and fished areas (Graham et al. 2008), indicating there is no evidence that Indian Ocean NTAs promote reef recovery (Graham et al. 2008). These findings were corroborated by the results of this study from the Granitic Seychelles, which showed that reefs even within protected areas are showing no evidence of recovery.

14 Advantages of the methodological and analytical approaches adopted

The community and population based methods used a number of informative variables, including taxon-specific colony density, surface area and population demographic parameters, as well as various taxonomic richness, dominance, equitability and rarity measures. This enables analysis of important aspects of a coral community and population size frequency distributions, as well as taxonomic richness, dominance, equitability and rarity. Surface area values in turn provide a useful means of estimating coral-built reef complexity. These proved to be a highly revealing means of interpreting coral communities.

Other studies have characterised coral communities across different reef sites based on dissimilarity tree diagrams of taxonomic composition (Turak et al. 2007). However the present study is the first spatial meta-analysis of coral community surveys that combines data from surveys of colony size distributions with information on taxonomic composition of colonies at different scales. Data were contributed to this study by collaborators to help identify investigative approaches that might be used in the analysis of a larger body of multivariate coral community data collected by the ongoing CCCR programme.

The large sample-by-taxa and/or sample-by-size cohort data arrays produced permit novel approaches to illustrating coral communities by graphical representations of size frequency distributions across taxa, and favour analysis using non-parametric multivariate methods. These analyses are capable of simplifying the high-dimensional complexity of the data obtained to identify and characterise significant differences between samples. The combination of high resolution coral community sampling and multivariate analyses provides a means of documenting details of community structure, and is highly sensitive to spatial and temporal differences.

The analytical routines provide a replicable framework for discriminating significant differences between sites and sample groups based on taxonomic and size frequency composition of taxa across large multivariate data matrices.

These findings highlight the practical limitations of more basic coral surveying methods – for instance approaches that do not discriminate colony size or taxa. The methods used identify changes to scleractinian communities that cannot be discernible by conventional benthic composition assessments. These include changes in the size frequency distributions and demographic parameters of populations within communities, as well as successional processes and changing patterns of relative abundance and dominance of taxa following disturbances.

Global R values, indicating the degree of dissimilarity of sample groups in ANOSIM testing, are generally low. This is to be expected given the large number of samples and variables examined. The global permutation analyses upon which these ANOSIM tests are based examine dissimilarities between 89 sites across 5 regions from 403 replicates (for adult colonies alone), based on up to 51 variables, and as such are inevitably affected by the spatial variability inherent within regions. Importantly, many of the global and pairwise R values are clearly and very significantly different from zero, showing that differences between individual sample groups are highly significant.

An additional cause of the low Global R values is the Madagascar Toliara region, which is not significantly different to any other region in terms of taxonomic composition (shown through the results of pairwise R comparisons). This is in part because of the low number of reef sites in this region (which resulted in low statistical power in the data), and also because Toliara's sites lie within the ordination spread of samples describing reef communities from the other regions, notably the relatively close Andavadoaka reef region. These two regions inevitably have the closest faunal similarities, forming part of the same geomorphological reef system in southwest Madagascar, approximately 200 km distant.

Across all regions, the broad distribution of reef communities also constrains the ability of multivariate SIMPER analysis to discriminate variables (taxa or size classes) responsible for the variation between sites. The bubble plots used to superimpose individual variables over the results of multivariate ordinations thus provide a more effective way of discriminating dominant variables.

14.1 Interpreting reef complexity

At a number of reef sites, values of total colony area exceeded the total surveyed 2-dimensional sample area, resulting in surface area values over 100% of the available quadrat or transect area. This result is not an anomaly, but rather may be attributable to two factors. Firstly, the edge effect (see section 15.1; page 231) may have resulted in a positive bias in coral density and surface area values. Secondly, and undoubtedly more significantly, the 10m² belt transect describes a 2-dimensional sample area within a habitat that is highly 3-dimensional.

The method used for measuring corals in this study records the surface area of colonies, which are rarely flat, but commonly highly structurally complex. For example, a spherical massive colony rising from the reef substratum has a much larger surface area than a flat colony of the same cross-sectional area. Many common reef surveying protocols, which estimate or measure levels of absolute cover of hard coral in 2-dimensions, fail to take into account this reef architectural complexity, and do not allow for benthic cover values to exceed 100% of a 2-dimensional sample area. By measuring corals individually across the colony surface to take account of colony area in a third dimension, the method adopted in this study effectively allows for a more realistic interpretation of coral surface 'cover'.

Comparison of conventional benthic cover variables against the total colony surface area variable developed in this study provides important insight into reef structural complexity. For example, two given reef sites may have similar values of 'conventional' coral cover, but very different values of total colony area, so it

could be inferred that the site with the higher difference between the two variables has higher three-dimensional complexity of corals.

Such differences can be seen in this study (Figure 43; page 129), and relate clearly to observed differences in coral community composition. For example, the two Granitic Seychelles sites Mahe West Granite and Mahe West Carbonate both showed similarly high levels of coral cover for the region (intercept transect values 19 ± 2 % SE and 22 ± 2 % SE respectively). Both sites were among the most pauperate reefs visited in the region, with relatively high abundance of adult colonies for the region (5.5 and 4.7 colonies m^{-2} for the granitic and carbonate site respectively). Both sites also showed higher values of total colony surface area than of 'conventional' coral cover, indicating that the coral assemblages showed a degree of architectural complexity beyond a 2-dimensional flat community. But the relative difference between the measures differed markedly; an approximately 1.5-fold increase at the granitic site, compared to an almost 7-fold increase at the carbonate site (Figure 43; page 129)(total colony surface area 30% and 146% of the 2-dimensional sampled area respectively).

Thus, despite having very similar 'conventional' coral cover and lower colony density than the granitic site, the carbonate site's community was by far the more structurally complex of the two. This is consistent with field observations; whereas the granitic site's adult coral community was characterised by a very high abundance of small colonies dominated by Faviidae (mean adult colony diameter 20.9 ± 0.5 cm SE), the carbonate site showed much greater structural complexity, with large poritiid and acroporid colonies, whose mean size was over twice that of the granitic sites (mean adult colony diameter 41.9 ± 2.2 cm SE). The conventional 'coral cover' : surface area ratio thus represents a new and effective measure of reef rugosity.

There is a caveat, however. All values of colony surface area measured in this research are likely to be under-estimated, since the single measurements taken of each colony approximate colony size are based on the largest diametric axis

across the surface of each colony. This approach assumes all colonies to have an approximately planar surface, which is clearly not the case; no branching, tabular, columnar or corymbose colonies conform to this highly simplified morphology, meaning that this approach, based on crude 'rubber-sheeting' colony measurements greatly underestimates both the surface area of polyps within the colony, as well as the three dimensional complexity of the corals. The relative error between real and measured colony areas is inevitably much greater in structurally complex taxa (such as *Pocillopora damicornis*) than in flat or massive taxa (such as *Porites lutea*). This means that the true coral colony surface area values are far greater than the values obtained in this research; in reality reefs inevitably show far higher 3-dimensional complexity, and thus a far greater difference between values of 'conventional' 2-dimensional benthic coral cover and total colony surface area.

14.2 Surveying cryptic and newly-metamorphosed juvenile colonies

Given the difficulties of seeing newly metamorphosed juveniles *in situ*, surveys of juvenile colonies normally under-represent the smallest size classes (generally under 10-30 mm colony diameter), due to difficulties in detecting small and cryptic colonies.

The trials of ultraviolet sampling were carried out to assess the proportion of juvenile coral colonies that might otherwise be overlooked. The technique elevated the numbers of juveniles across all size categories, with the proportion of this increase (relative to those colonies detected through 'visual light' census) increasing with decreasing colony size. This resulted in profound changes to the shape of the size frequency distribution of colonies recorded. These results confirm that a large cohort of newly-metamorphosed juvenile recruits usually escapes detection in conventional visual surveys.

It is likely that colony crypsis within this cohort is responsible for the initial increase in colony abundance with size typically observed in conventional 'visual light' juvenile colony surveys between colony size classes 1 and 3 (Figure 73; page 170). This observed increase is not consistent with known trends of coral

demography, where colony size-frequency distribution within a coral population is normally highly positively-skewed, dominated by progressively smaller size classes. Data obtained through UV census reflect the expected demographic trends more correctly, the results of this study therefore give a compelling indication of the utility of the UV method in more accurately monitoring the smallest cohorts within coral communities.

Given that surveying newly-settled recruits on natural substrata is rarely practical, the results of this study indicate that surveying of juvenile coral distribution and abundance using the UV method may be used as surrogate indicator for settlement and recruitment rates.

14.3 AAC curves

The abundance/area comparison (AAC) curves plotted in Figure 62 (page 111) are based on the concept of the abundance/biomass comparison (ABC) method of determining levels of disturbance on benthic macrofaunal communities (Clarke and Warwick 2001), using colony genus surface area data as a surrogate for species biomass. This enables testing of the standard ABC assumption, namely that within unperturbed communities biomass (surface area) is dominated by few large taxa, leading to a raised biomass (surface area) curve, which lies above the abundance curve for its whole length. This curve is then assumed to become progressively lower in relation to the abundance curve with increasing environmental disturbance (as a result of differential survivorship and mortality of large taxa versus numerically-dominant small taxa) eventually falling below the abundance curve.

Given the sampling design of this study, in which it was not possible to include either experimental spatial control samples, or within-region temporal comparisons following environmental disturbance, the AAC plots provide a useful means of interpreting relative degrees of disturbance to between samples, both within and between regions.

14.4 Benefits of methodology relative to other approaches to surveying adult corals

Past studies of coral communities have employed diverse sampling designs, criteria for 'adult' and 'juvenile' colonies, and methodologies for measuring and recording corals. The wide variation in published methods used to sample and describe juvenile and adult hard coral communities prevents detailed like-for-like comparison of the findings of this study with past research. At best, comparisons of relative colony abundance or taxonomic dominance are possible (Appendix V, Table 15; page 270). The relative merits, constraints and bias of different sampling approaches, compared to the techniques employed in this research, warrant further discussion.

14.4.1 Benthic composition surveys

Coral colony sampling carried out here is more detailed than the more conventional and widely-used reef benthic surveying techniques, such as intercept or quadrat surveys, which typically measure relative cover across broad benthic and substrate categories, but rarely capture information on the structure or density of coral communities, let alone populations within them. In contrast, this research captured many key ecological benchmarks of coral communities, favouring a more detailed interpretation of the ecosystem.

For example, widespread evidence of recent reef mortality was observed at almost half of the sites surveyed in the Farasan Banks, Saudi Arabia. Multivariate analysis of data derived from benthic composition estimates of these data failed to discriminate impacted sites from those that had not experienced mortality. In contrast, analysis based on data from these coral surveys showed significant separation of mortality-affected sites, whether based on adult colony abundance or surface area data across taxa. These differences were even more significant when the taxonomic variables were substituted for colony size classes. The inability of simple benthic composition data to detect such a severe and fairly recent ecological disturbance in multivariate analysis highlights a striking limitation to the sensitivity of that widely used approach. Clearly, the enhanced

sensitivity of the alternative method employed in this study reduces the likelihood of a type II statistical error of this nature.

The failure of the juvenile coral surveys carried out in this study to detect the presence or absence of reef mortality in the Farasan Banks does not indicate a comparative lack of sensitivity of juvenile colony data in detecting disturbance, relative to the adult colony surveys. Rather, it emphasises an important benefit of obtaining data from the separate colony size cohorts; namely that in this case, the lack of agreement between juvenile and adult colony data in discriminating sites based on evidence of reef mortality strongly supports the conclusion that recruitment is not a limiting factor preventing reef recovery of impacted reefs in the Farasan Banks (section 11.1.1; page 192).

Again, this shows that the lack of agreement between the results of coral community surveys and benthic composition estimates in detecting mortality in the Farasan Banks highlights another limitation of the widely used benthic composition methods, which assesses coral cover over a theoretical 2-dimensional area. Measurements of total colony surface area (as a percentage of transect area) at the Farasan Banks varied by a factor of 28 between the highest and lowest site values, with a standard deviation across all sites of 43% (Figure 42; page 129). Mortality-affected sites were clearly detectable based on analysis of these data. In contrast, estimates of benthic cover failed to detect the mortality at affected sites; values of coral cover between the same sites differed by only a factor of 3, with a standard deviation across all sites of 12%.

This considerable difference is partly because conventional benthic cover methods assess relative coral cover, which can never exceed 100%, whereas measurements of total colony surface area record the absolute coral surface area across the same site. Whilst relative coral cover from benthic cover estimates can never exceed 100%, absolute coral surface area, when measured from a structurally complex reef, will frequently exceed 100% of the 2-dimensional surface area of the transect as a result of corals growing in three dimensions, such as on vertical surfaces or even two sides of the same 2-dimensional surface.

In other words, two reefs with very different values of absolute colony surface area could record the same estimates for benthic coral cover, but have vastly different coral habitat; for example if the reef with the higher value of colony surface area also showed a higher structural complexity. Conversely, for a fixed total colony surface area, as reef complexity increases, percentage coral cover decreases. This is a severe limitation to the conventional methods, which, as has been shown, cannot effectively identify otherwise marked differences in the Farasan Banks.

14.4.2 Sampling only target 'indicator' taxa, and grouping measurements by size classes

The results show that restricting coral surveying to a reduced community of pre-defined target genera, as is used by the CCCR methodology, does not impede comparative multivariate analyses of sites based on generic composition. Indeed limiting the target taxa does not reduce the power of the data to discriminate between sites and samples, even when the number of genera sampled is reduced by over 60%. Moreover, reduction of the number of target taxa inevitably liberates survey time to enable collection of a larger sample of commoner corals, facilitating more accurate analysis of demographic parameters within populations of these target taxa.

However these findings also indicate that this reduced taxa approach greatly limits the extent to which between-sample differences may be observed based on taxonomic richness. When analysed across samples within a survey region, measures of taxonomic richness provide important insight into ecological disturbance, as demonstrated by the higher generic richness and higher equitability of taxa observed at Farasan Banks sites that had not experienced mortality relative to those that had. This reduced taxa approach also prohibits studies of taxonomic rarity, and it is conceivable that the disappearance of rarer taxa as a result of disturbance might be unobserved as a result.

Furthermore, grouping colonies into pre-defined size class bins reduces the resolution of size frequency distribution analysis, and thus reduces the accuracy of population demographic parameters calculated from assemblage measurements. Together, the selection of a reduced community of target genera and limiting colony measurements to size classes therefore represents a tradeoff between permitting a larger reef area or number of replicate samples to be obtained, and the greater benefits gained from the ability to detect potentially ecologically-significant aspects of taxonomic richness and diversity.

14.4.3 Inferring colony size from intercept transects

Several approaches to surveying coral communities have inferred size frequency distribution of different coral taxa through the relationship between the contribution of each coral taxon to the total benthos (measured for example through benthic line intercept surveys) and the frequency of colonies of each genus (measured for example through a line or belt transect)(Riegl and Velimirov 1994). Any approach that infers colony size from an intercept transect is likely to yield less accurate demographic data, since a much larger sample size would be required to account for the effect of colony intercepts that do not cross the longest axis of the colony.

For example, if a line intercept transect were to pass over a small peripheral outgrowth of a large colony of massive *Porites*, the resulting intercept value would record the length of that segment alone, not the maximum diameter of the entire colony. Thus the resulting size measurement for this colony would be highly inaccurate – as it would for any others where the line intercept did not, by chance, cross the longest diametric axis of the colony.

14.4.4 Relative abundance surveys

Another widely used ‘rapid assessment’ method for estimating coral bleaching in the Indian Ocean enables assessment of relative abundance of coral genera (McClanahan et al. 2004; McClanahan 2008). Although effective for rapid sampling and requiring no measuring equipment for field surveys, this approach does not record any spatial dimensions of either corals or sample areas, thus ruling out calculation of colony size, population demographic parameters or

colony density and/or surface area per unit area. This greatly limits the extent to which resulting data can be used to infer coral community composition, since relative abundance or dominance of a taxon is in no way related to absolute abundance or dominance of that coral; as shown in this study, colony density varied between sites and regions by up to 75-fold in adult corals and up to 470-fold in juvenile corals (7.1.1; page 94).

For example, a number of highly depauperate sites in the Granitic Seychelles showed relative abundances of taxa similar to values from sites in other regions, whereas actual abundance values were profoundly dissimilar. Across ten replicate transects at the Granitic Seychelles site 'Praslin Southwest Carbonate', *Acropora* accounted for 25% of adult colonies recorded. This relative abundance of *Acropora* is identical to that recorded at Farasan Banks reef site number 15. However the absolute density of *Acropora* at the two sites differed a massive 175-fold; from 0.02 colonies m⁻² at the Seychelles site to 3.50 colonies m⁻² at the Farasan Banks site.

Finally, size-independent measures of colony frequency values provide no means of determining colony area – arguably a far more pertinent indicator of the contribution of taxa to a coral community, and also of the architectural complexity of a coral reef.

14.5 Benefits of methodologies used relative to other approaches to surveying juvenile corals

14.5.1 Quadrat size

Surveys of juvenile corals in this study demonstrated their remarkable crypticity, even when above 3 cm in size. In shallow water, corals generally settle on vertical or under-surfaces (Rogers et al. 1984), and even an experienced surveyor can frequently overlook colonies of considerable size. In addition to the challenges of observing cryptic colonies, recording all juvenile colonies within a survey quadrat can be challenging as a result of high colony abundance. Some samples in this study recorded over 20 colonies within a single 33 cm by 33 cm quadrat (0.11 m²). At such sites, accurately identifying and measuring all

colonies can be demanding. Surveying similar sites across a larger sample area, such as 1m by 1m, would be extremely difficult and time consuming, if not practically impossible, and may result in significant bias through under-recording or double-counting of corals, the latter a problem identified in past studies (Miller et al. 2000).

The larger 1 m² quadrat favoured by the CCCR approach may therefore have resulted in depressed juvenile colony values, confounding differences relative to values recorded in this study. For instance, colony density values from the Farasan Banks, Saudi Arabia, recorded in this study are approximately double those recorded in at Al Wajh and Yanbu by collaborators using the larger 1 m² quadrat (66.1 compared to 36.3 colonies m⁻²). This is despite adult colony density being lower at the Farasan Banks than Al Wajh (7.2 compared to 11.3 colonies m⁻²). The effect of quadrat size cannot however be tested from the data - examination of the effect of use of different quadrat sizes on colony abundance values within the same reef habitat would be required to establish the existence and extent of this potential error.

14.5.2 Non-random sampling of substrata for juvenile corals

Some previous approaches to surveying juvenile corals focused sampling efforts only on 'settable' substrata; typically placing sample quadrats only on substrata on which corals are able to settle, defined as "either parent rock or carbonate that is free from macroalgae, live hard and soft coral, sessile invertebrates and excessive sediment" (Wilson 2007). Other methods exclude samples that contain more than one substrate type, or mature coral colonies (Sheppard et al. 2002).

In this research, quadrats were placed randomly on the reef, regardless of the nature or degree of colonisation of the underlying substratum. Quadrats would inevitably often be placed on unsuitable substrata, such as entirely within the surface of a living coral, or on an exposed 'unsuitable' sandy patch (Figure 84a and b). In such cases the number of recruits recorded would be zero, and the effect of this 'blank' quadrat would be reflected in the resulting values of juvenile colony abundance per unit area for that site, since site values were calculated

based on pooled data from all replicates in that site. This random sampling approach is considered preferable to the biased sampling method described above because the biased approach cannot give an accurate indication of juvenile colony density (absolute juvenile colony abundance per unit area); rather this approach only measures colony abundance on exposed 'settleable' surfaces. This research has shown that overall juvenile colony abundance is correlated to the amount of settleable substratum. Therefore total colony abundance values, per unit area, are clearly influenced by the amount of exposed substrate.

Moreover, the definition and selection of substrata deemed suitable for settlement are highly subjective, thus difficult to standardise and potentially highly variable between studies. In addition, this method is equally dependent on the surveyor finding a sufficiently large area of unoccupied substratum on which to place a survey quadrat. Therefore, as well as being subject to variations in the amount of exposed unsettled substrata, results of this approach are also likely to be an artifact of quadrat size. For example, at many sites in the Farasan Banks where coral cover and structural complexity were very high, had this approach been adopted it would not have been possible to find an entirely unsettled area on which to place a 33 cm x 33 cm quadrat – surveying at such sites necessitated sampling coral-dominated areas with little available unoccupied substratum, and where recruits could often only be found by carefully scrutinising crevices and holes between corals.

These differences in survey methods employed between this research and past studies limit the value of comparisons of data between studies. For example, Wilson (2007) recorded juvenile colony density values in Chagos higher than those observed in this study (70 colonies m^{-2} \leq 50cm maximum diameter compared to 15 colonies m^{-2} ; Appendix V, Table 15; page 270). However this comparison is likely to be misleading, since Wilson (2007) only surveyed 'bare' areas of reef surface, causing the inevitable effect of boosting resulting density values. This research shows that restricting sampling to 'settleable' substrata only is likely to greatly increase the number of juveniles observed per sample, therefore detailed comparison of these studies is not meaningful.

14.5.3 Photographic sampling of juvenile corals

Other methods of sampling juvenile corals rely on the results of retrospective analysis of photographs of quadrats. This technique is sometimes favoured because of the underwater survey time saved by not needing to identify and measure colonies *in situ*. This technique was trialled during this study in Chagos, however it was quickly abandoned when comparative studies of the two approaches showed that only a small proportion of coral colonies could be observed retrospectively, and few of those could be identified accurately to genus level, even with the use of high-resolution macro photography and image analysis software. This is because of the cryptic nature of most small corals, which preferentially select hidden or vertical surfaces for settlement, thus prohibiting detection.

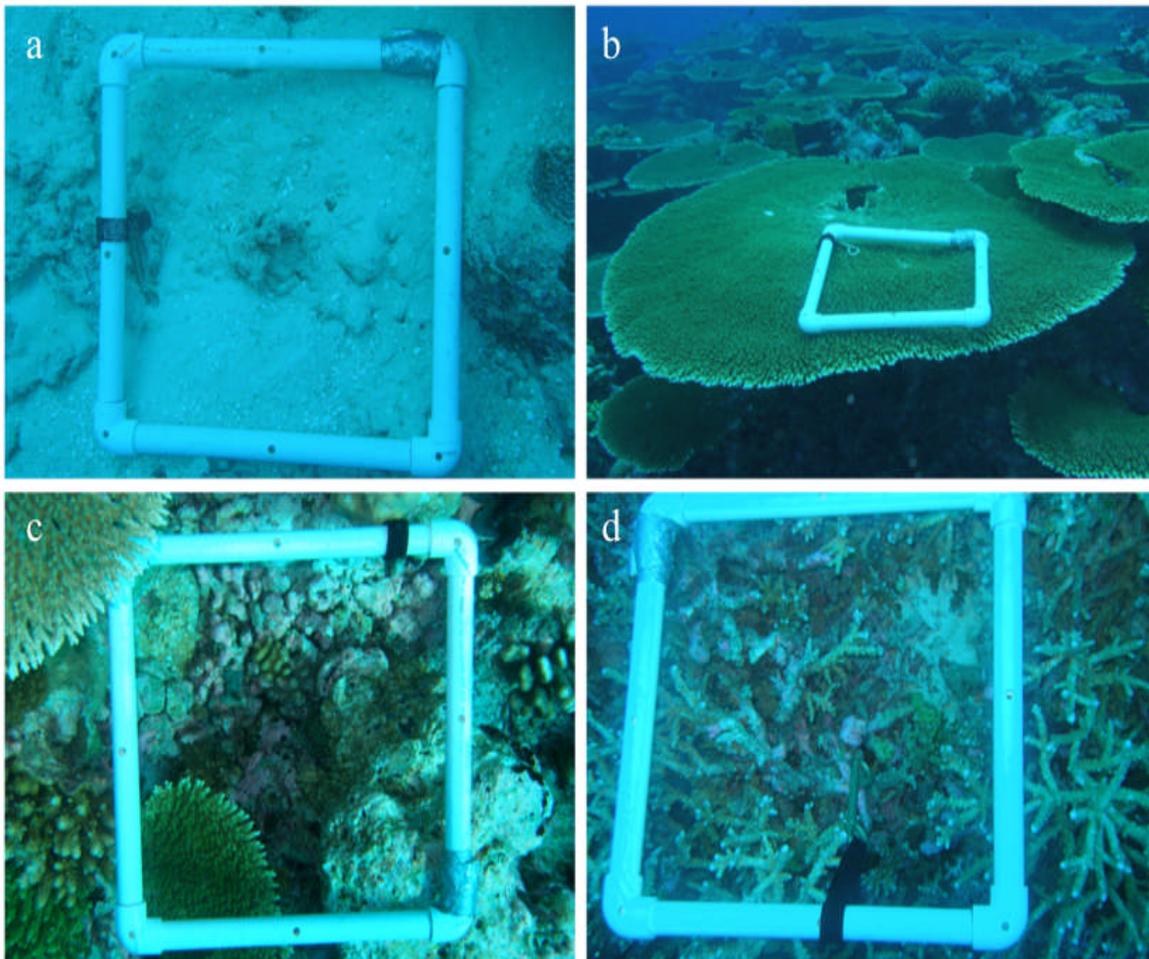


Figure 84(a) and (b). Examples of 'blank' juvenile quadrats; (c) and (d) examples of challenges of surveying juvenile colonies from photographs. 20 corals $\leq 10\text{cm}$ were recorded *in situ* in the quadrat shown in (c)

To illustrate the severe limitations of this approach, the area contained within the 33 cm x 33 cm quadrat shown in Figure 84c, surveyed in the Chagos Archipelago *in situ*, contained 20 juvenile corals under 10 cm in size. Fewer than half of these are detectable in the photograph. Figure 84d further illustrates the challenges to detecting juvenile corals from photographs from structurally complex benthic habitats. In this case, it is not possible to examine the shaded or hidden areas of this quadrat from the photograph. The limitations of the accuracy of using photo-quadrats to survey juvenile corals identified during this research are consistent with other critiques of this technique (Edmunds et al., 1998).

15 Potential sources of bias and limitations of sampling and surveying methodology

15.1 “Edge effect”

The sampled area within transects included corals crossing the transect margin where more than 50% of the total colony surface area lay inside the 10 m² belt. Where a colony crosses a transect margin it is assumed that there is an equal likelihood of that colony lying predominantly either inside or outside the transect boundary. For this reason, it is also assumed that, across replicate transects, any increase or decrease in colonies resulting from inclusion or exclusion of these ‘boundary colonies’ will approximately balance, returning to an overall 10 m² sample area.

Nevertheless, within a 10 m x 1 m belt transect it is theoretically possible for sampling to include additional corals within a skirt of 50 cm width running around the boundary of the 10 m² transect. If this skirt were to be filled entirely with contiguous ‘boundary colonies’ lying predominantly inside the transect area, the method would result in sampling an additional area of 12 m² around each 10 m² transect. This ‘edge effect’ is of course extremely unlikely, but may have resulted in a positive bias for observations of recorded colony density and surface area.

Varying the transect length would change the potential impact of this variability relative to the intended sample size. For example, using a shorter transect length of 8 m x 1 m would reduce the potential additional skirt to 10 m²; a relatively much greater potential bias, which could result in a larger potential error relative to the belt size. The opposite is true for a longer transect, where the relative seriousness of this edge effect would be reduced. All transects carried out in this study were 10 m in length, therefore it is assumed that any bias resulting from the edge effect is approximately equal across all reef sites and regions. However, the variable transect length permitted in the CCCR sampling methodology may result in greater between-site variability in survey bias resulting from this edge effect.

In addition to bias attributable to the boundary skirt, size-biased selection may have occurred as a result of the sampling methodology causing bias in the colony density and demographic parameter measurements recorded. Misrepresentation of coral communities could occur if, for example, colony density were identical between two reef sites, but mean colony size was larger at one site than the other. In this case the site with the larger colonies would yield a higher estimate of colony density per unit area than the second, because of the larger number of colonies crossing the sample (quadrat or transect) boundary. Thus the larger a colony, the higher the likelihood of that coral intersecting or falling partly within the boundary of a belt transect or quadrat. Care was taken to remove edge effects in belt and quadrat sampling by only counting corals as belonging to a sample if more than 50% of the colony area fell within the sample area, however despite this precaution size-biased selection may have resulted in non-random sampling around transect edges. Caution must therefore be taken when interpreting the findings of this study in terms of providing values of true colony density and demographic parameters, although the calculations obtained herein are likely to be very close to the true values. Moreover, given that the sampling and methods employed in this study were consistent across all survey regions, observations drawn from between-site comparisons remain valid, and legitimate conclusions may be inferred from like-for-like comparisons of sites and regions relative to one another.

15.2 Inconsistencies in sampling effort

The sampling area required to record the first colony of a coral genus is approximately inversely proportional to the relative abundance of that genus. The Bray-Curtis similarity coefficients that form the basis of the MDS ordinations and ANOSIM tests detect patterns of change in presence and absence of taxa between sites, combining this with information on the changing numerical coral density (or surface area) at those sites. Transformation of raw data puts decreasing emphasis on high abundance values and increasing emphasis on presence/absence values. Increasing replication of samples within each site therefore inevitably leads to higher numbers of genera, as shown by genus accumulation curves (7.6.2.1; page 159), which illustrate the relationship between sampling effort and the number of taxa.

The observation of increasing between-sample dissimilarity with increasing within-sample (reef site) sampling effort (replicate transects/quadrats)(Figure 54; page 148) necessarily required thorough testing during multivariate analysis (7.5.2.4; page 147), to ensure that between-sample differences observed were not an artefact of sampling effort.

However, although between-sample dissimilarity increased with increasing sampling effort, the observed differences in community composition at Granitic Seychelles reef sites (median 10 replicate transects per site compared to median 2 replicates at all other regions, and 90 replicate quadrats per site, compared to 46 at Chagos and 5 at Saudi Arabia) were attributed to real differences in community structure, rather than being an artefact of sampling effort, since subsequent retesting for between-region differences using raw replicates (rather than pooled replicates per reef site) maintained the significance of between-region differences.

Nevertheless, the importance of standardising replicate numbers per reef site (or region) wherever possible should be emphasised in future research continuing the techniques used in this study.

15.3 Partial colony mortality

Definitions of the term coral colony differ between studies. In this study, in order to be consistent with other authors (Bak and Meesters 1998), a coral was not recorded as two separate colonies if partial mortality had resulted in separation of two areas of the same formerly continuous living tissue. However certain other studies, including McClanahan *et al.* (2008), define a colony as a coral with continuous unbroken tissue. This difference in colony definition would result in a marginal increase in colony abundance values in studies that define colonies as areas of continuous living tissue.

Partial colony mortality is an extremely important factor influencing coral size frequency distributions, having been shown to account for as much tissue loss from corals over time as total colony mortality (Hughes and Jackson, 1985). Corals experience differential susceptibility to partial mortality based on colony size and environmental stress – factors that varied considerably between reef sites and regions in this study.

Although partial mortality is likely to have played a role in structuring the coral communities and populations examined in this research, the methodology adopted in this study did not address this factor. Ideally, future research could measure partial tissue mortality for each colony surveyed by recording a qualitative estimate of proportional surface area mortality, to enable incorporation of this important factor in the analysis process, and to enable examination of variability of partial mortality across regions, taxa and colony sizes.

15.4 Suitability of substratum for settlement

Coral recruits preferentially settle on certain hard substrata; notably rock, uncolonised dead coral, or encrusting calcareous algae. Certain substrata, such as loose coral rubble, are less favourable to juvenile coral survival, since water movements can easily move them. At survey regions in south-western Madagascar, many sites showed large areas of dead *Galaxea fascicularis* which, following mortality, had eroded into a porous highly mobile rubble that had not

been consolidated. Qualitative assessments of juveniles at these sites indicated that this substratum prohibited effective recruitment of corals. Large areas of unconsolidated coral rubble were also present at Granitic Seychelles reefs, where this undoubtedly played a role in limiting coral regrowth. Conversely, the large expanses of exposed granite at many other Granitic Seychelles reefs (Jennings et al. 1996), and the broad areas of uncolonised dead corals at many Farasan Banks reefs, undoubtedly favoured settlement by juvenile colonies. Similarly, at several sites in Chagos, intact dead *in situ Acropora* tables were observed to support notably more juvenile corals than other substrata.

These observations suggest that the nature of a reef's dominant coral taxon prior to a mortality event (and thus the composition of a reef's settlement substratum following a mortality event) can determine the subsequent recovery potential and trajectory of the reef following mortality; some south-western Madagascar reefs, formerly dominated by *Galaxea fascicularis*, appear to be unfavourable to recolonisation by juvenile corals, whereas in the Granitic Seychelles, corals growing directly on a hard granitic rock substrate proved very suitable for coral settlement.

Unfortunately this hypothesis cannot be tested, since no record of the underlying substratum was recorded during surveys of juvenile corals gathered during this research. Future assessments of juvenile coral communities could thus benefit from a modified methodology, recording the nature of the settlement substratum for each colony surveyed.

15.5 Variation with depth

Given the increasingly adverse impacts of temperature stress in driving broad-scale changes in coral communities, understanding responses of coral communities and populations at different depths within the same ecosystem may provide insight into the relative responses of corals to different temperature regimes. Different depths also exhibit different coral assemblages, adapted to different levels of temperature and UV light variability, exposure, sedimentation and stress.

For example, studies of coral communities at Cosmoledo Atoll in the Aldabra group of islands in the southern Seychelles in 2002 showed that differences between the generic composition of adult and recruit communities were less at deeper sites, which did not experience such heavy mortality in 1998. Sheppard and Obura (2004) hypothesise that these deeper communities were located below a critical 'transition depth' of 10m at Cosmoledo; a thermocline between upper waters where corals were virtually eliminated in 1998, and deeper waters where coral mortality was less severe (Sheppard and Obura 2005; Obura et al. 2006). Repetition of the research undertaken in this study at different depth profiles would permit investigation of depth-dependent disturbances to coral communities, greatly improving understanding of zonal susceptibility of coral communities to disturbance.

15.6 Definition of juvenile

Classification of juvenile and adult colonies based on size, across all taxa, is entirely arbitrary and varies between studies. The 10 cm definition used in this research was chosen to ensure direct comparability of results with the Indian Ocean CCCR research project (IUCN-World Conservation Union), from which comparative data were obtained. This categorisation is based on the need to differentiate colonies based on size between the two sampling techniques used (belt transect and quadrat), since it is not generally feasible to sample juvenile colonies across a reef area as large as 10m² using SCUBA. This nomenclature refers purely to the size of the corals in question and does not infer any aspect of the sexual maturity of corals surveyed: it is of course accepted that post-pubescent colonies of many taxa may be considerably smaller than 10cm.

The majority of comparable studies of juvenile cohorts of corals select a cut-off between 5 and 10cm maximum diameter; colonies above 5cm diameter are usually sexually mature and therefore may be classified biologically as adults (Miller et al. 2000). The analysis approach used in the present study enabled filtering of juvenile data to 'reduce' this maximum size, for comparative analysis with other studies that employed a smaller size definition for juveniles, such as Wilson (2007)(Figure 83; page 205).

However, the use of different sampling approaches for surveying juvenile and adult colonies presents a major limitation to analyses of demographic parameters across whole coral populations. Juvenile and adult colony data cannot easily be 'mixed' to produce a continuous data set accounting for all size cohorts within a population or community; in this study the unit area used for sampling juvenile corals (33 cm by 33 cm quadrat) was 99 times smaller than that used to sample adults (1,000 cm by 1 cm belt). Therefore all demographic statistics calculated in this study were based only on adult data. This prohibits comparison of adult colony demographic parameters against studies that may have used a different definition of 'juvenile' (McClanahan et al. 2008).

The paucity of recent data of coral demography and size frequency dynamics emphasises the importance of standardisation of monitoring methodologies between future studies wherever possible, to facilitate future geographical and temporal comparisons of observations.

15.7 Taxonomic accuracy

This study identified corals to genus level only, pooling colony size measurements for all species within genera. Certain genera contain clear species that differ greatly in size, vulnerability to mortality, structural complexity, rarity and geographic range occurrence. The presence or absence of an unusually large or small species within any genus at one region would inevitably influence demographic data gathered for that taxon compared to other regions. For example, the methodology adopted in this research did not differentiate between branching colonies of *Porites matthai* and massive colonies of the same genus, such as *P. solida* or *P. lutea*. Similar variation in colony size and growth form is seen within numerous genera, including the common and often dominant taxa *Echinopora*, *Acropora*, *Pocillopora* and *Pavona*.

Species also show a great deal of morphological plasticity depending on environmental conditions, which were not constant between study regions. For example, the highly oligotrophic, steep gradient reef slopes typical of Farasan Banks and Chagos oceanic reefs present very different conditions for coral

growth to the shallow and frequently turbid conditions typical of many continental shelf fringing reefs in the Granitic Seychelles and Madagascar, which, in this study, were generally located on horizontal or gently sloping substrata. The environmental conditions typical of the Granitic Seychelles favour small encrusting growth forms of *Echinopora gemmacea*, whereas on the near-vertical reef slopes of the Farasan Banks, the same species commonly adopts large plating colonies, often with branching elements that dominate the benthic faunal community.

Together, these factors constrain the accuracy and utility of comparative demographic analyses based on generic populations. This limitation could be addressed by surveying colonies to species level, but this would greatly reduce the statistical power of resulting demographic analyses, by substantially reducing the number of colonies recorded within each taxon.

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Appendix I: genus-specific bubble plots

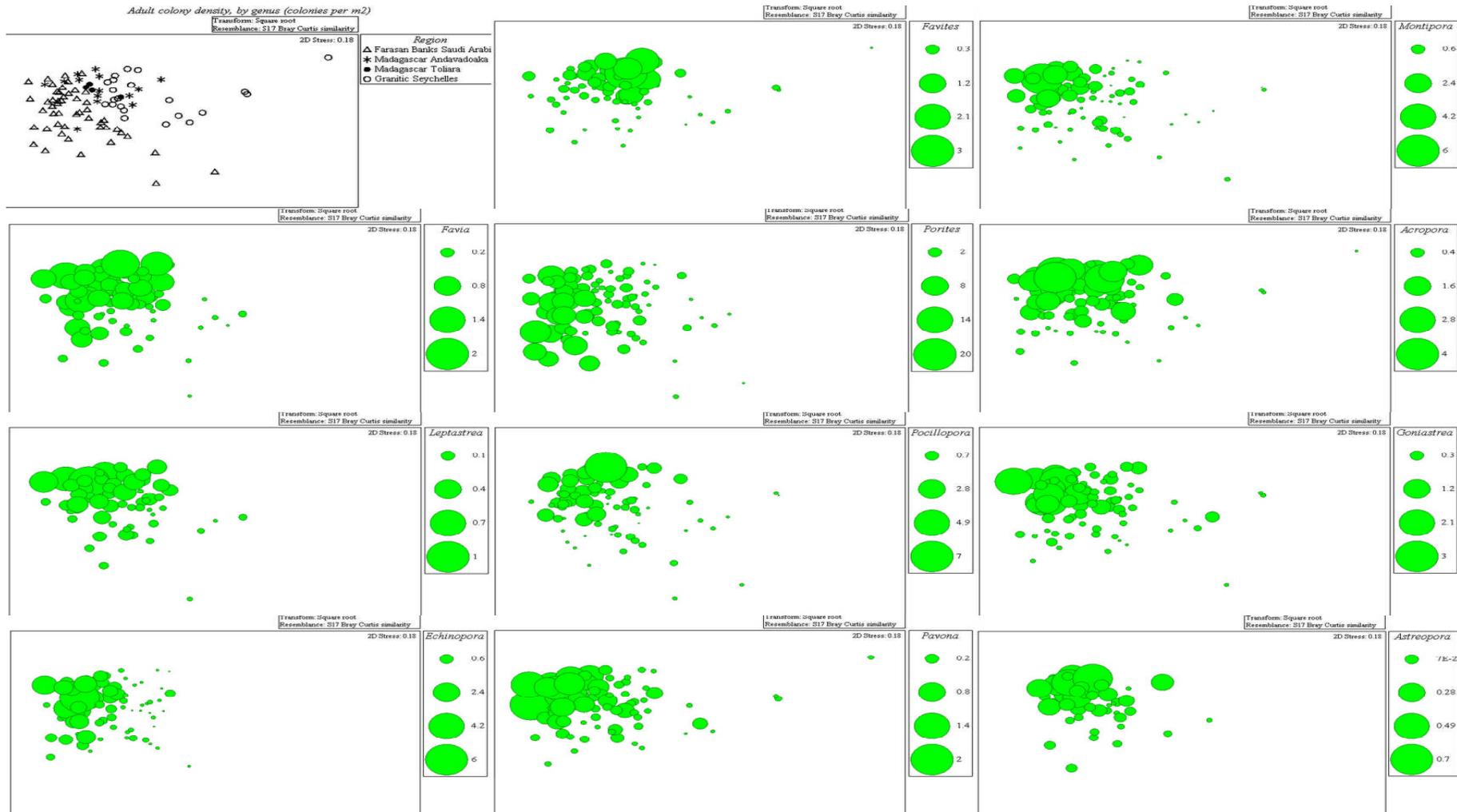


Figure 85. Genus specific adult colony density variables superimposed on non-metric MDS plots of adult coral density data based on all taxa, all sites & regions

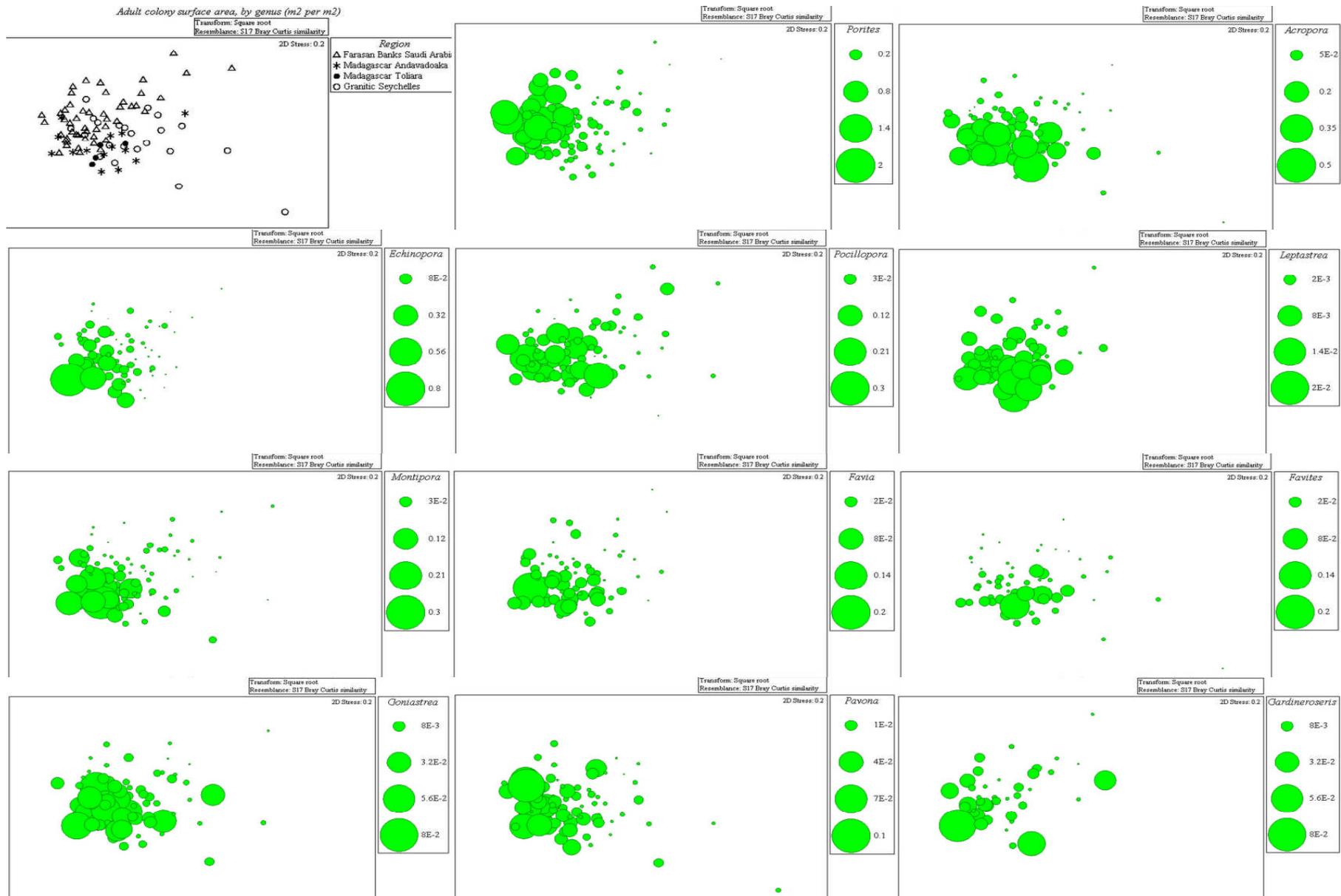


Figure 86. Genus specific adult colony surface area variables superimposed on non-metric MDS plots of adult coral surface area data based on all taxa, all sites & regions

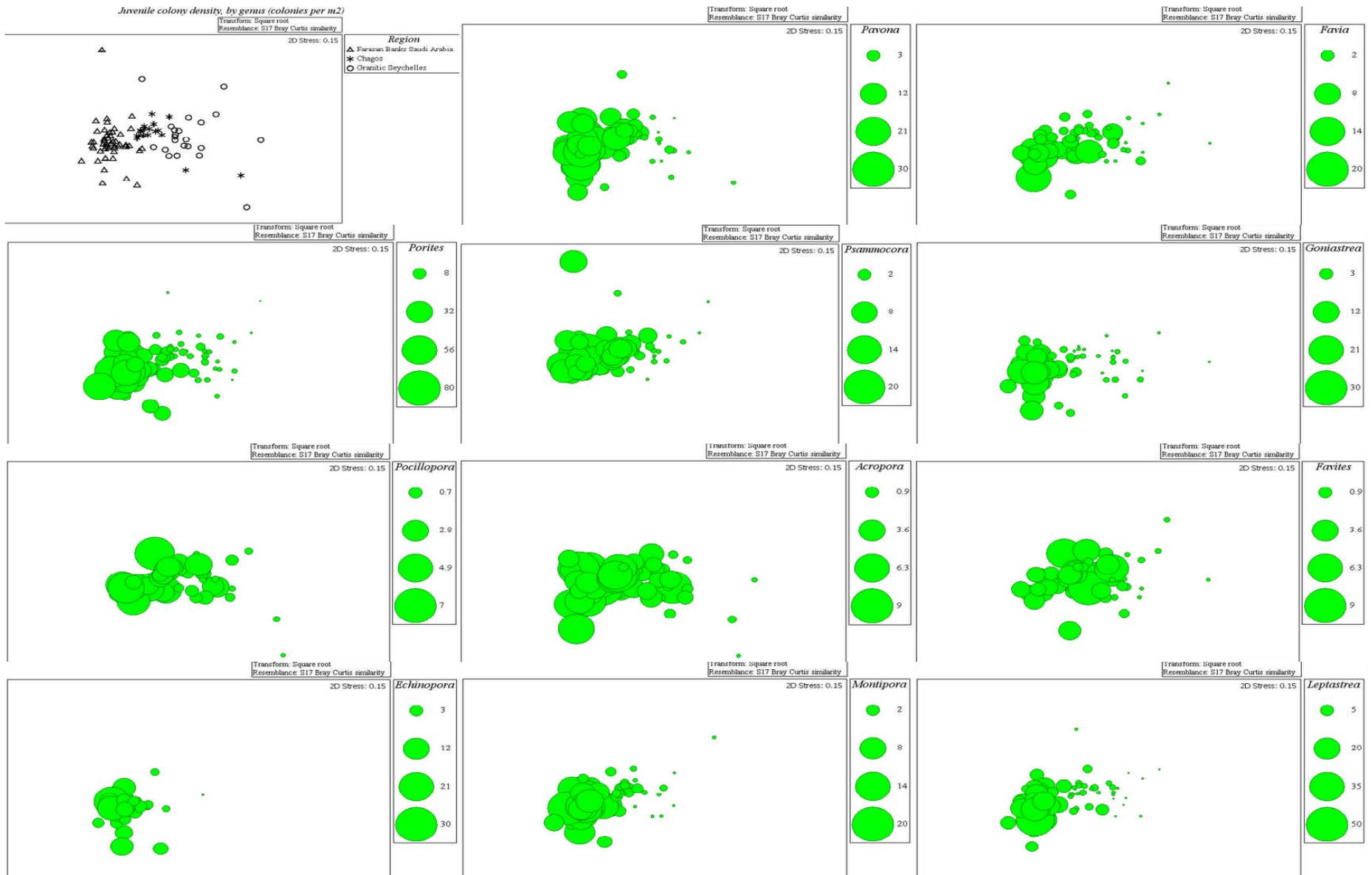


Figure 87. Genus specific juvenile colony density variables superimposed on non-metric MDS plots of juvenile coral density data based on all taxa, all sites & regions

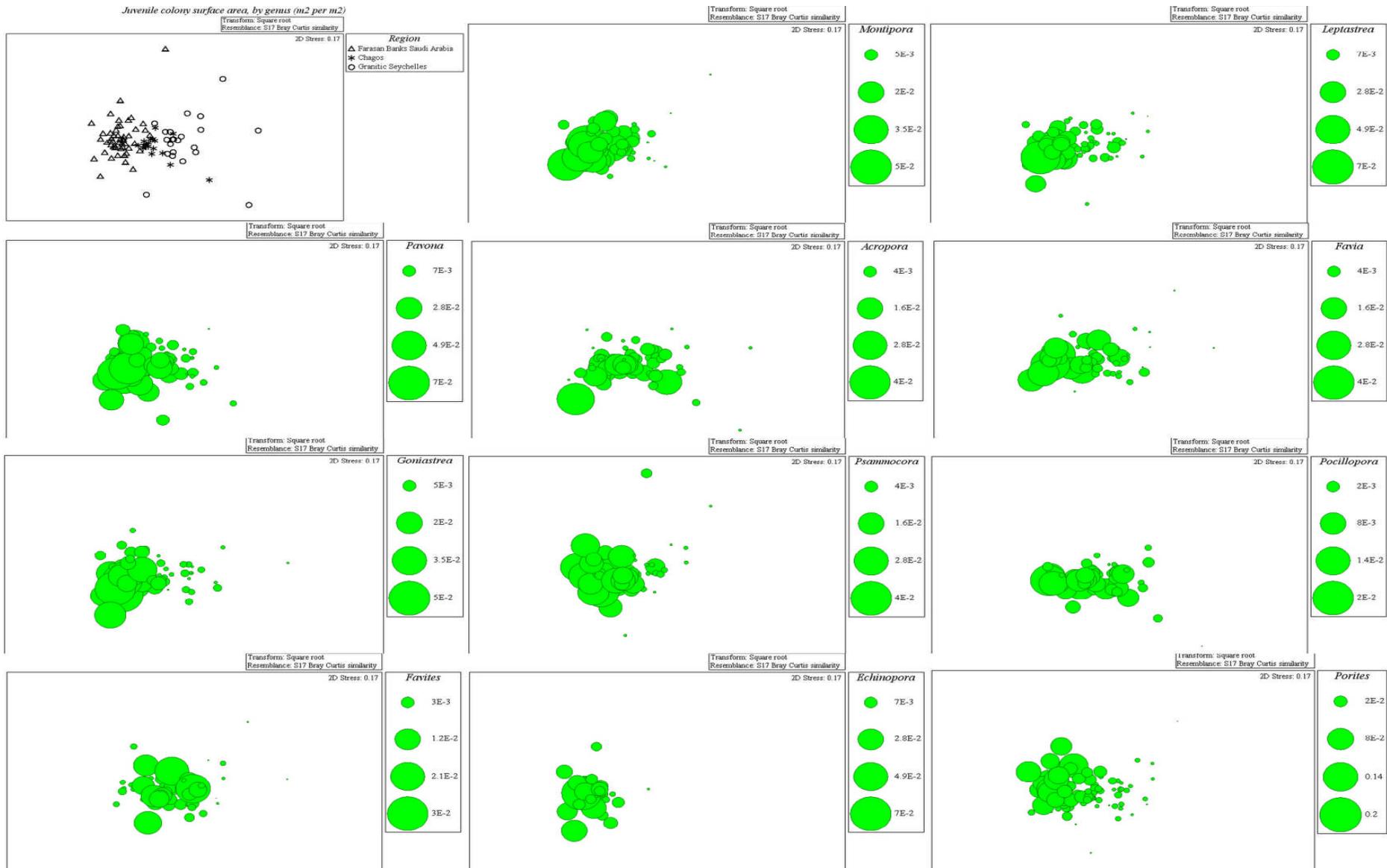


Figure 88. Genus specific juvenile colony surface area variables superimposed on non-metric MDS plots of juvenile coral surface area data (all taxa, sites & regions)

Appendix II: genus specific mean colony sizes, by region

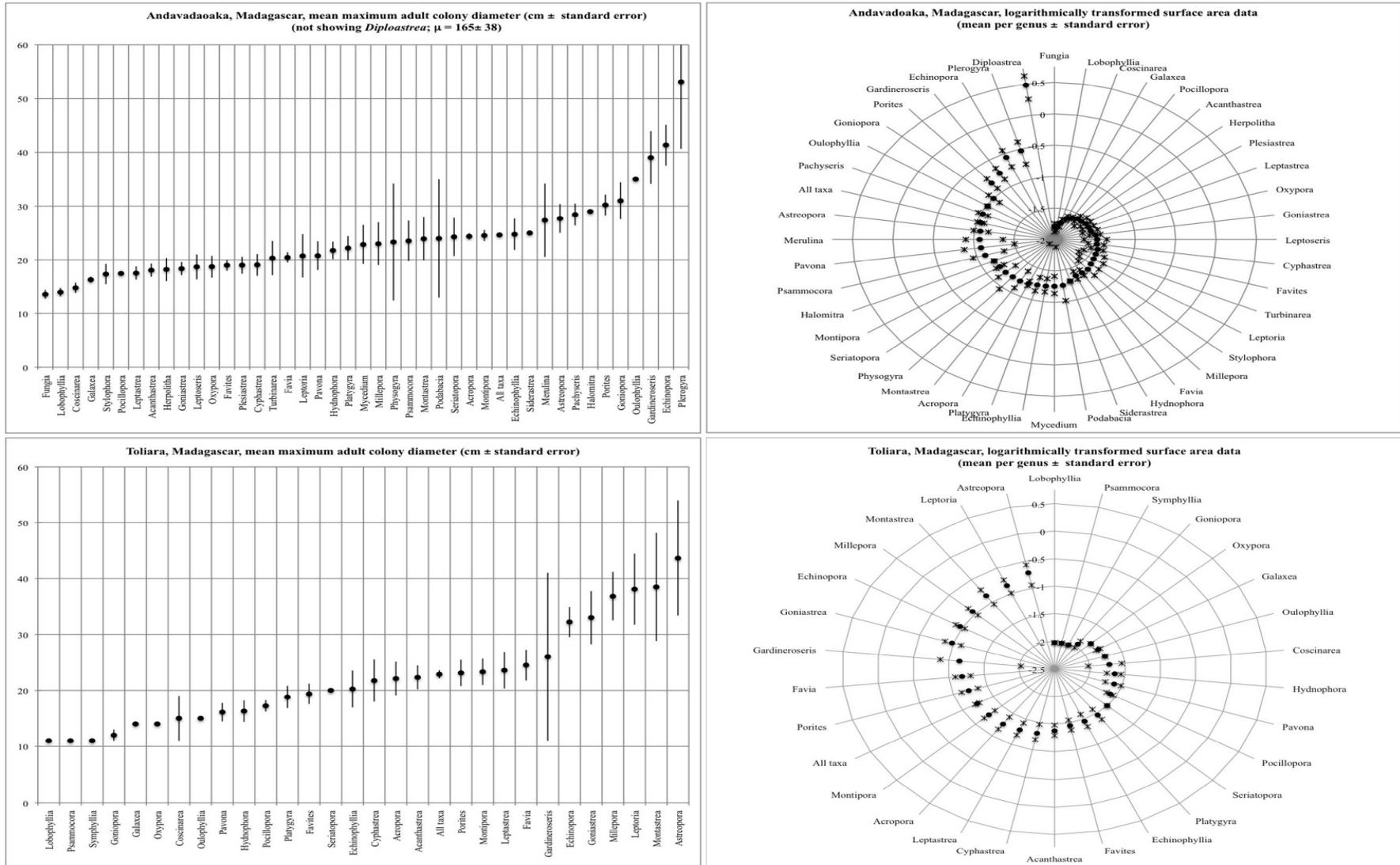


Figure 89. Mean colony diameter and logarithmically transformed surface area per genus (± standard error of mean): Toliara & Andavadoaka, SW Madagascar

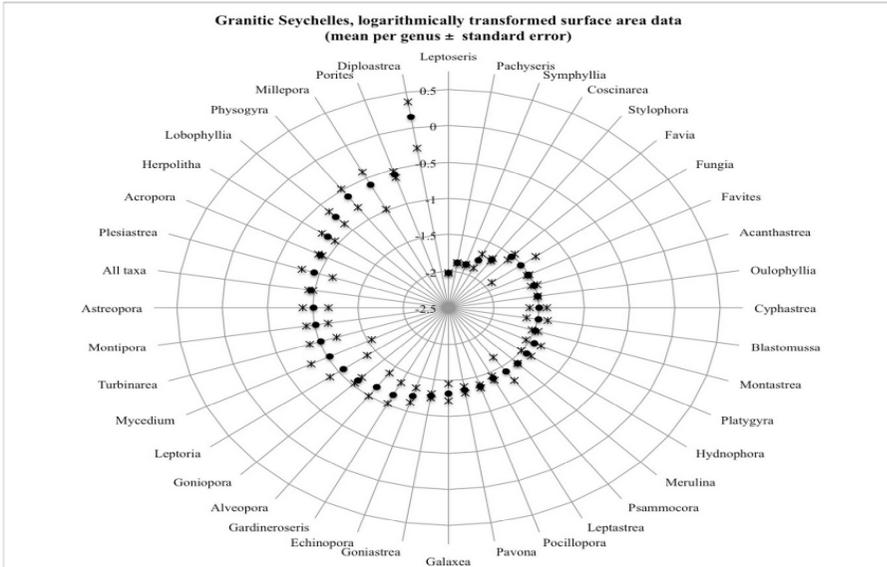
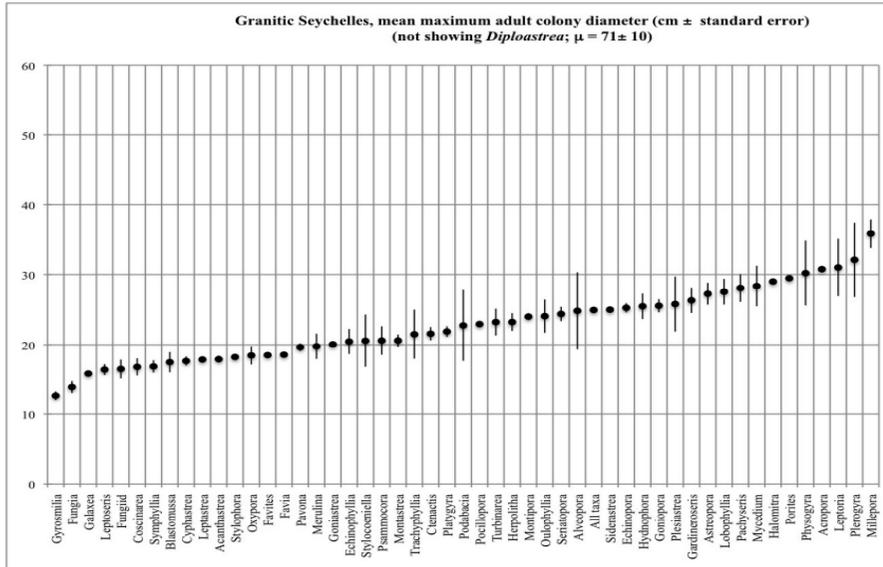
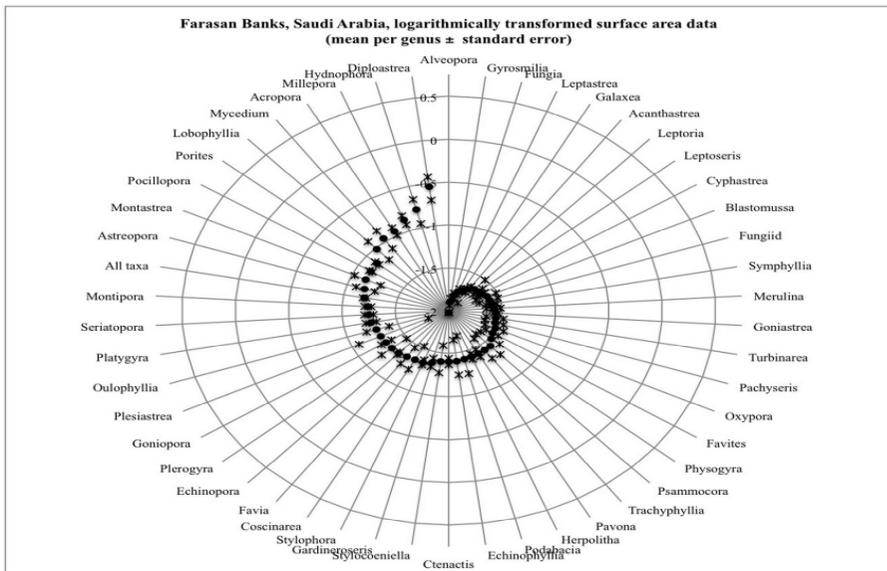
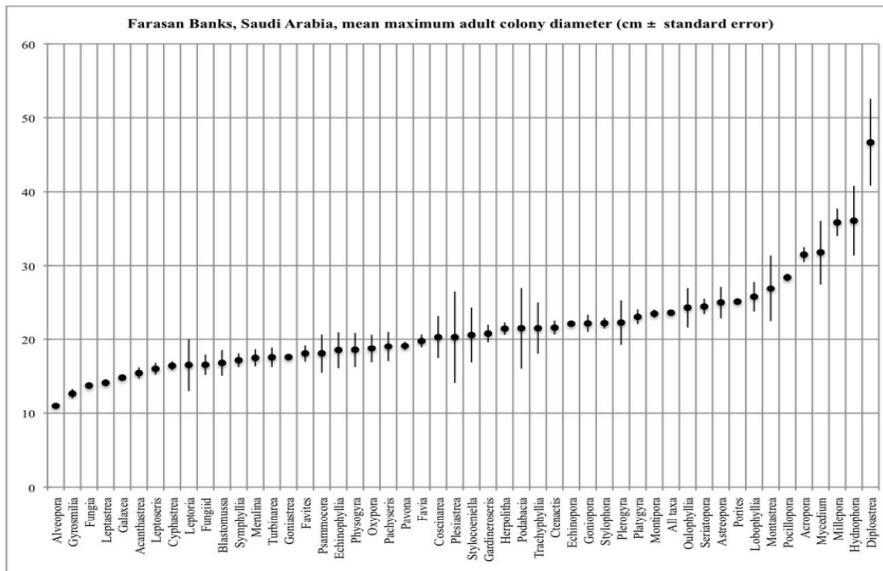


Figure 90. Mean colony diameter and logarithmically transformed surface area per genus (\pm standard error of mean): Farasan Banks & Granitic Seychelles

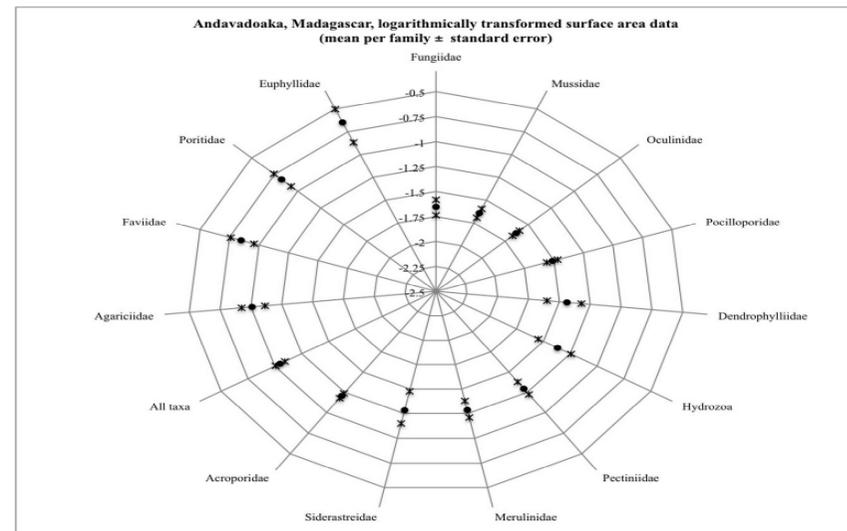
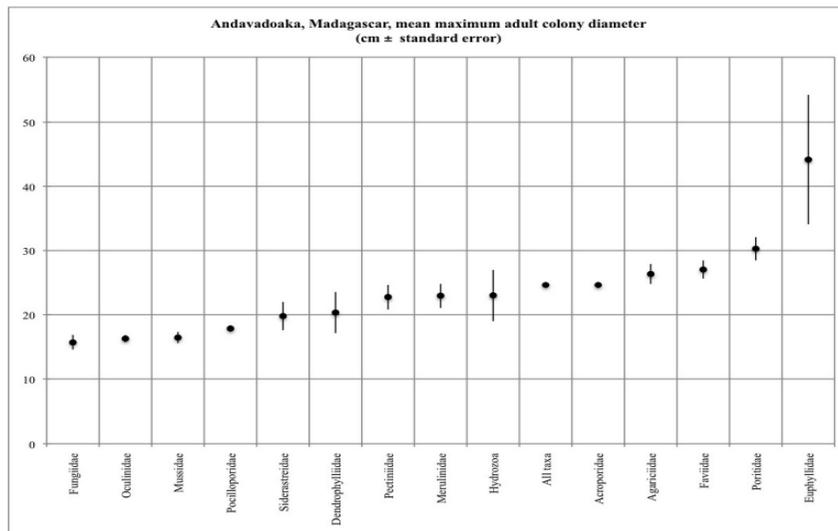
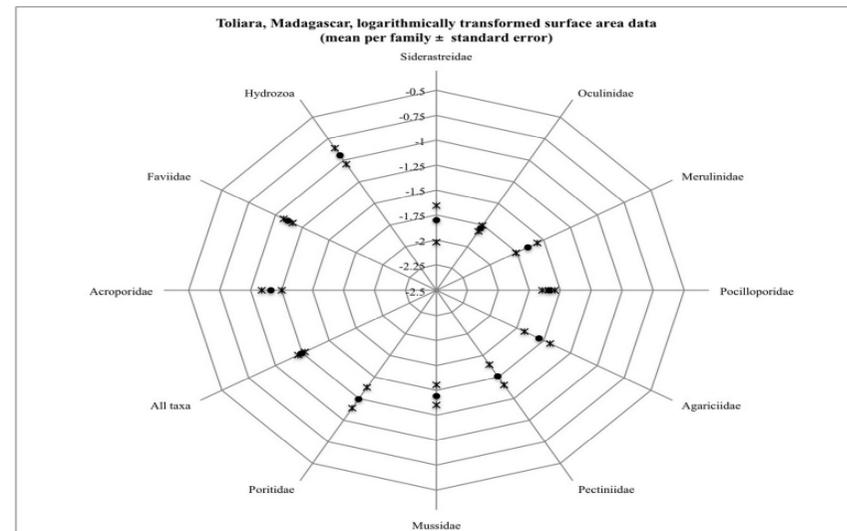
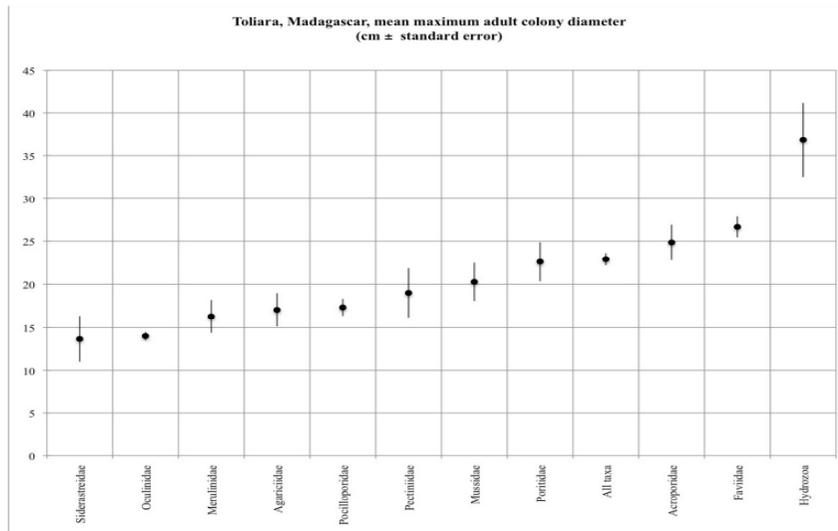


Figure 91. Mean colony diameter and logarithmically transformed surface area per family (± standard error of mean): Toliara & Andavadoaka, SW Madagascar

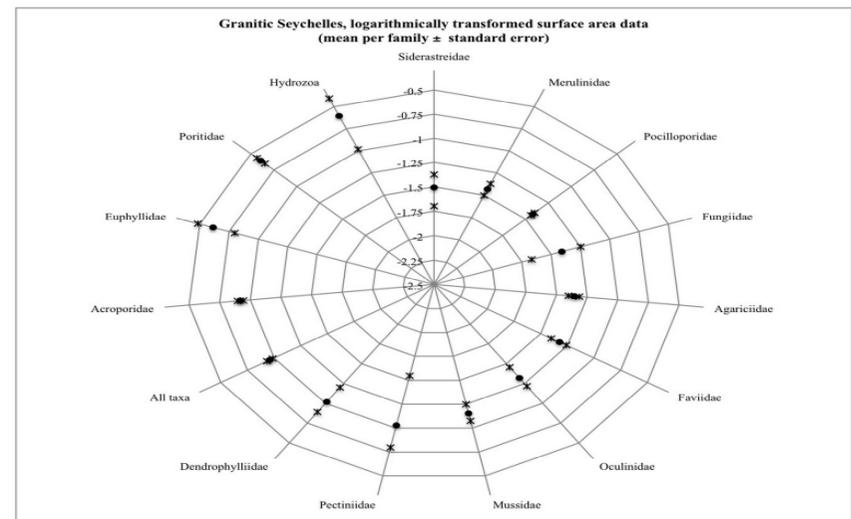
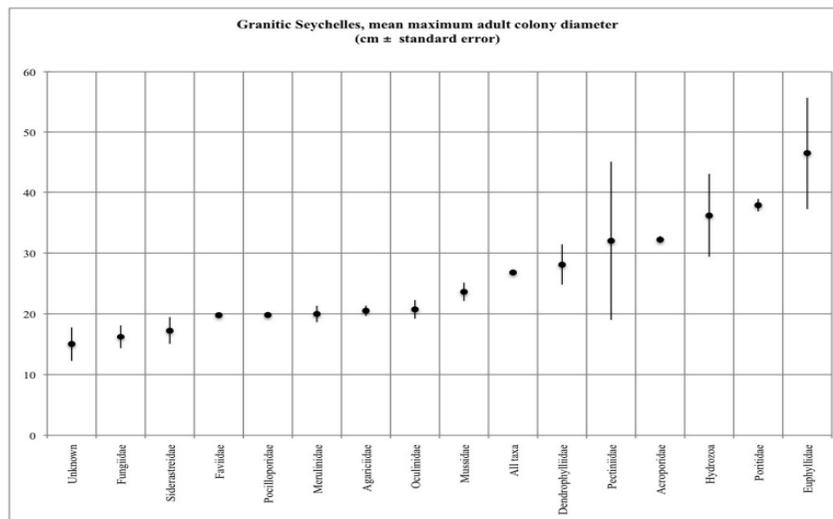
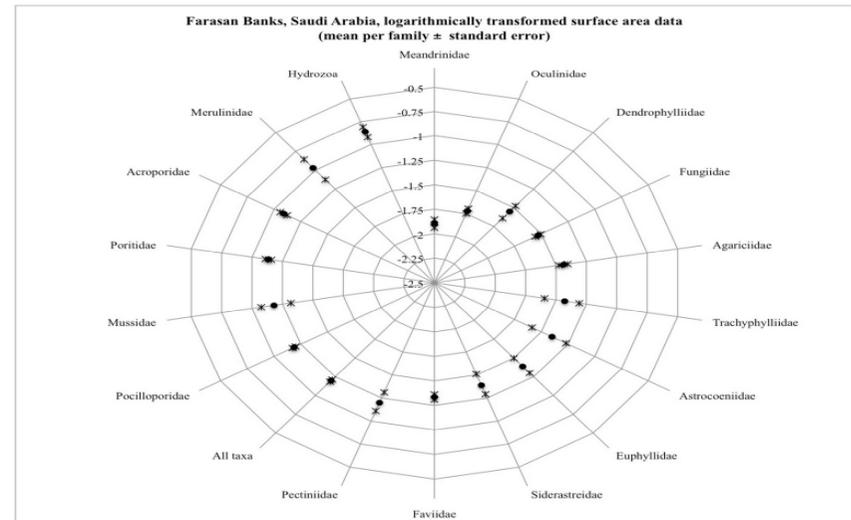
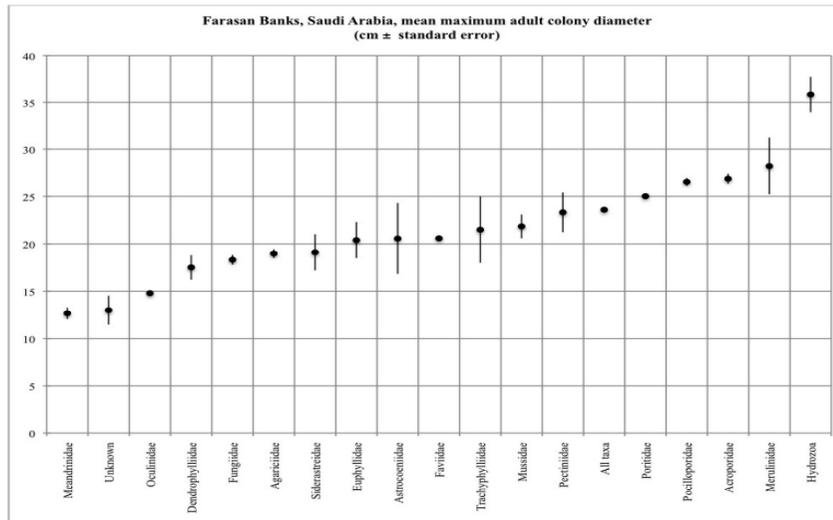


Figure 92. Mean colony diameter and logarithmically transformed surface area per family (± standard error of mean): Farasan Banks & Granitic Seychelles

Appendix III: generic demographic distribution parameters (by survey region)

Table 12. Distribution parameters of colony size of all corals (>10cm maximum diameter) data and logarithmically transformed surface area data for all genera across 4 survey regions (continued overleaf)

Genus	Region	N	Maximum colony diameter (cm)								Logarithmically transformed colony surface area									
			Mean	Std. Error of Mean	Minimum	Median	Maximum	Kurtosis	Std. Error of Kurtosis	Skewness	Std. Error of Skewness	Mean	Std. Error of Mean	Minimum	Median	Maximum	Kurtosis	Std. Error of Kurtosis	Skewness	Std. Error of Skewness
Acanthaster	Aradenoloka Madagascar	17	18.06	1.214	11	18.00	27	-0.95	1.863	448	550	-1.6248	0.0830	-2.00	-1.8021	-1.24	-1.058	1.063	0.90	0.550
	Faranon Banko Soudi Ambia	44	15.41	0.550	11	13.00	28	-0.96	1.702	1.849	357	-1.7871	0.0822	-2.00	-1.8951	-1.21	-0.890	1.02	0.767	0.357
	Grande Ile Seychelles	106	18.58	0.719	11	15.50	44	0.11	1.465	1.262	233	-1.6255	0.0893	-2.00	-1.7218	-0.82	-0.490	0.465	0.704	0.233
	Tolara Madagascar	9	22.33	2.121	16	21.00	37	3.459	1.400	1.878	717	-1.4345	0.0718	-1.70	-1.4559	-0.97	1.542	1.400	1.884	0.717
	Total	176	17.93	0.511	11	16.00	44	1.338	1.364	1.584	183	-1.6530	0.0218	-2.00	-1.8990	-0.82	-0.460	0.364	0.588	0.183
Acropora	Aradenoloka Madagascar	427	24.37	0.897	11	22.00	144	26.713	2.56	3.999	118	-1.4123	0.0340	-2.00	-1.4202	21	0.707	2.296	5.58	1.18
	Faranon Banko Soudi Ambia	459	31.47	0.997	11	27.00	232	27.908	2.27	4.952	114	-1.2388	0.0200	-2.00	-1.2441	63	0.603	2.227	4.81	1.14
	Grande Ile Seychelles	1391	32.68	0.803	11	27.00	269	13.819	1.53	2.797	0.66	-1.2255	0.0328	-2.00	-1.2441	73	-2.24	1.33	4.46	0.66
	Tolara Madagascar	24	22.13	2.593	11	18.00	65	2.465	0.918	1.732	472	-1.5500	0.0448	-2.00	-1.8990	-0.48	1.03	0.918	1.822	0.472
	Total	2271	30.76	0.436	11	25.00	269	18.674	1.03	3.176	0.51	-1.2884	0.0078	-2.00	-1.3966	73	0.99	1.03	5.34	0.51
Atrypa	Faranon Banko Soudi Ambia	1	11.00	-	11	11.00	11	-	-	-	-	-2.0000	-	-2.00	-2.0000	-2.00	-	-	-	-
	Grande Ile Seychelles	5	27.60	5.802	17	28.00	48	5.32	2.099	1.255	0.93	-1.2927	1.8841	-1.84	-1.5096	-0.74	-0.974	2.099	0.93	0.93
	Total	6	24.80	5.408	11	28.00	48	5.30	1.741	1.180	0.85	-1.4306	1.8102	-2.00	-1.5096	-0.74	-1.58	1.741	0.85	0.85
Astropora	Aradenoloka Madagascar	44	27.70	2.683	11	22.50	87	1.843	1.702	1.447	357	-1.3886	0.0760	-2.00	-1.3985	-2.3	-0.818	0.702	0.97	0.57
	Faranon Banko Soudi Ambia	51	25.00	2.168	11	21.00	84	4.222	0.656	1.946	233	-1.4327	0.0696	-2.00	-1.4559	-2.0	-0.038	0.656	0.90	0.33
	Grande Ile Seychelles	54	27.22	3.685	14	19.00	137	11.019	0.659	5.975	325	-0.4604	0.0658	-2.00	-1.5528	17	1.733	0.659	1.332	0.325
	Tolara Madagascar	6	43.67	10.285	15	38.50	80	-1.414	1.741	4.59	0.45	-0.991	2.2385	-1.74	-0.614	-0.50	-1.208	1.741	-2.36	0.45
	Total	155	27.26	1.557	11	21.00	137	7.833	0.87	2.382	1.95	-1.3853	0.0372	-2.00	-1.4559	17	0.92	0.87	0.93	0.95
Blastomussa	Faranon Banko Soudi Ambia	13	16.77	1.723	11	15.00	33	3.845	1.191	1.635	616	-1.7023	0.0760	-2.00	-1.5447	-1.07	-0.65	1.191	0.98	0.616
	Grande Ile Seychelles	5	19.40	2.057	11	21.00	27	-1.344	2.000	-3.01	0.93	-1.3643	1.3635	-2.00	-1.4559	-1.24	-0.914	2.000	-0.91	0.93
	Total	18	17.50	1.460	11	16.00	33	2.703	1.838	1.044	0.674	-1.6648	0.0741	-2.00	-1.8915	-1.07	-0.608	1.638	0.95	0.56
Coccyzonia	Aradenoloka Madagascar	25	14.80	0.838	11	13.00	27	2.169	0.802	1.756	464	-1.7989	0.0631	-2.00	-1.8861	-1.24	1.143	0.802	1.442	0.464
	Faranon Banko Soudi Ambia	21	28.29	2.865	11	15.00	62	4.591	0.972	2.155	501	-1.6111	0.0572	-2.00	-1.5447	-0.52	0.46	0.972	1.255	0.501
	Grande Ile Seychelles	7	14.14	1.580	11	12.00	22	3.885	1.587	1.297	0.794	-1.8231	0.0858	-2.00	-1.8586	-1.42	-1.70	1.587	1.831	0.794
	Tolara Madagascar	2	13.00	4.060	11	13.00	19	-	-	-	-	-1.7764	2.2358	-2.00	-1.7364	-1.55	-	-	-	-
	Total	55	16.82	1.234	11	14.00	62	11.766	0.64	3.109	322	-1.7299	0.0448	-2.00	-1.8239	-0.52	1.072	0.64	1.720	0.322
Ctenactis	Faranon Banko Soudi Ambia	43	21.58	0.951	11	22.00	34	-0.877	0.706	1.52	361	-1.4756	0.0434	-2.00	-1.4202	-1.04	-0.813	0.709	-0.338	0.361
	Total	43	21.58	0.951	11	22.00	34	-0.877	0.706	1.52	361	-1.4756	0.0434	-2.00	-1.4202	-1.04	-0.813	0.709	-0.338	0.361
	Aradenoloka Madagascar	18	19.06	2.035	11	15.00	38	1.04	1.838	1.151	536	-1.6285	0.0338	-2.00	-1.7614	-0.95	-0.781	1.038	0.756	0.536
Cypastrea	Faranon Banko Soudi Ambia	67	18.39	0.947	11	15.00	38	5.585	0.776	2.049	293	-1.7088	0.0521	-2.00	-1.5447	-0.95	1.328	0.776	1.147	0.293
	Grande Ile Seychelles	47	17.91	1.544	11	14.00	62	11.351	0.81	2.930	347	-1.6726	0.0480	-2.00	-1.8239	-0.52	2.368	0.81	1.421	0.347
	Tolara Madagascar	12	21.75	3.756	11	15.00	45	-1.178	1.232	1.771	637	-1.5611	1.4231	-2.00	-1.7933	-0.80	-1.885	1.232	5.13	0.637
	Total	144	17.67	0.660	11	15.00	62	7.831	0.81	2.434	202	-1.6541	0.0547	-2.00	-1.7447	-0.52	1.328	0.81	1.564	0.202
	Aradenoloka Madagascar	9	165.90	37.830	35	178.00	385	3.77	1.400	1.743	717	1.034	2.088	-1.02	0.661	1.07	-1.153	1.400	0.661	0.717
Diploria	Faranon Banko Soudi Ambia	44	46.70	5.898	11	38.50	206	6.260	1.702	2.325	557	-0.828	0.0655	-2.00	-0.9587	52	-0.958	0.702	3.58	0.557
	Grande Ile Seychelles	20	84.90	23.897	11	42.50	488	10.118	0.992	2.902	512	-0.7074	0.0604	-2.00	-0.8544	1.26	-0.553	0.992	3.70	0.512
	Total	73	71.75	9.781	11	43.00	488	8.347	0.55	2.813	381	-0.7734	0.0334	-2.00	-0.8586	1.26	-0.312	0.55	0.98	0.381
Ectocarpus	Aradenoloka Madagascar	13	24.37	2.914	11	22.00	49	0.865	1.191	0.94	616	-1.3443	0.0760	-2.00	-1.2441	-0.72	-0.97	1.191	-1.34	0.616
	Faranon Banko Soudi Ambia	28	18.50	2.442	11	15.00	80	20.442	1.858	4.271	441	-1.6888	0.0785	-2.00	-1.5447	-0.50	3.385	1.858	2.281	0.441
	Tolara Madagascar	4	28.25	3.361	11	22.50	25	1.134	2.819	-1.337	1.914	-1.5321	1.8287	-2.00	-1.4992	-1.31	2.140	2.819	-1.553	1.914
	Total	45	28.87	1.785	11	17.00	80	13.717	0.695	3.188	554	-1.5799	0.0552	-2.00	-1.8285	-0.50	3.855	0.695	1.133	0.554
Echinopora	Aradenoloka Madagascar	123	41.58	3.085	11	28.00	357	25.327	4.53	4.102	218	-1.1288	0.0600	-2.00	-1.2076	1.00	1.51	4.53	0.90	0.218
	Faranon Banko Soudi Ambia	727	22.11	0.421	11	19.00	89	4.578	1.81	1.895	0.91	-1.5033	0.0391	-2.00	-1.5528	-2.1	-0.82	1.81	0.724	0.091
	Grande Ile Seychelles	55	24.26	2.260	11	22.00	80	7.852	0.778	2.226	308	-1.4352	0.0600	-2.00	-1.4202	-0.50	0.014	0.778	0.432	0.308
	Tolara Madagascar	59	32.22	2.784	11	27.50	80	1.54	0.662	0.988	337	-1.2327	0.0753	-2.00	-1.2259	-0.80	-1.057	0.662	1.48	0.337
	Total	935	25.26	0.657	11	20.00	357	85.624	1.60	6.624	0.80	-1.4383	0.0454	-2.00	-1.5086	-1.30	1.378	1.60	1.831	0.080
Favia	Aradenoloka Madagascar	158	20.46	0.847	11	18.50	69	4.687	1.60	2.049	206	-1.5885	0.0540	-2.00	-1.6660	-0.43	0.77	1.60	1.576	0.206
	Faranon Banko Soudi Ambia	245	19.76	0.89	11	18.00	191	80.023	3.10	7.982	156	-1.6023	0.0230	-2.00	-1.8990	46	3.457	3.10	1.399	0.156
	Grande Ile Seychelles	510	17.13	0.432	11	15.00	143	73.716	2.16	6.958	1.08	-1.7825	0.0314	-2.00	-1.5447	21	6.068	2.16	1.869	0.108
	Tolara Madagascar	31	24.52	2.739	11	19.00	70	3.841	0.821	1.594	421	-1.4588	0.0232	-2.00	-1.5528	-0.41	-0.81	0.821	0.90	0.421
	Total	924	18.57	0.384	11	15.00	191	71.217	1.61	6.400	0.80	-1.6521	0.0123	-2.00	-1.5447	46	3.527	1.61	1.559	0.080

**(Table 12
continued)**

Genus	Region	N	Maximum colony diameter (cm)									Logarithmically transformed colony surface area								
			Mean	Std. Error of Mean	Minimum	Median	Maximum	Kurtosis	Std. Error of Kurtosis	Skewness	Std. Error of Skewness	Mean	Std. Error of Mean	Minimum	Median	Maximum	Kurtosis	Std. Error of Kurtosis	Skewness	Std. Error of Skewness
Favites	Arabavakolia Madagascar	96	18.98	1.807	11	16.00	87	22.478	485	3.535	246	-1.6227	0.3268	-2.89	-1.9976	-2.27	2.422	485	1.272	246
	Famusa Banksi Sraak Arabia	53	18.04	1.122	11	15.00	51	4.553	444	1.975	327	-1.6589	0.4434	-2.80	-1.7447	-1.60	2.541	444	1.049	327
	Gracilaria Seychelles	1094	18.48	2.13	11	17.00	65	6.522	148	2.004	874	-1.6227	0.8980	-2.80	-1.6580	-1.40	2.943	148	1.725	874
	Toliana Madagascar	24	18.58	1.836	11	15.00	45	1.806	918	1.395	472	-1.6677	0.7279	-2.80	-1.7447	-1.80	2.498	918	1.725	472
	Total	1267	18.51	2.07	11	17.00	87	18.574	137	2.363	869	-1.6240	0.8813	-2.80	-1.6783	-2.23	2.648	137	2.797	869
Fungia	Arabavakolia Madagascar	20	13.66	.822	11	13.00	27	9.490	892	2.812	512	-1.8581	0.4089	-2.80	-1.8860	-1.24	6.114	892	2.235	512
	Famusa Banksi Sraak Arabia	73	14.77	.576	11	13.00	80	11.384	335	3.017	281	-1.8088	0.2588	-2.80	-1.8860	-1.90	4.365	335	1.889	281
	Gracilaria Seychelles	63	14.16	1.779	11	12.00	128	38.883	804	7.607	396	-1.8874	0.3512	-2.80	-1.9588	0.03	43.140	804	6.138	396
	Total	154	14.38	2.60	11	13.00	138	104.376	389	9.520	995	-1.8427	0.6946	-2.80	-1.8860	0.03	26.600	389	4.158	995
Gobios	Arabavakolia Madagascar	187	14.31	.552	11	13.00	47	8.142	465	2.399	234	-1.7211	0.2808	-2.80	-1.7447	-1.76	1.319	465	1.262	234
	Famusa Banksi Sraak Arabia	339	14.80	.368	11	13.00	64	36.332	272	4.467	337	-1.7947	0.0183	-2.80	-1.8860	-1.89	8.540	272	1.889	337
	Gracilaria Seychelles	79	26.72	1.508	11	18.00	113	27.384	535	4.425	271	-1.5729	0.4285	-2.80	-1.9021	0.06	2.429	535	1.230	271
	Total	597	14.60	.477	11	13.00	25	1.711	630	1.513	330	-1.8250	0.2564	-2.80	-1.8860	-1.71	2.706	630	1.265	330
Gardineroclis	Arabavakolia Madagascar	33	39.03	4.889	11	29.00	169	-3.08	1.988	499	-1.3278	0.9379	-2.80	-1.1800	-1.08	-1.125	2.785	262	4.499	
	Famusa Banksi Sraak Arabia	77	26.78	1.184	11	17.00	48	-4.49	1.541	692	-1.5641	0.4555	-2.80	-1.6380	-1.74	-1.125	3.541	584	2.754	
	Gracilaria Seychelles	3	29.06	5.332	22	26.00	30	-	1.346	1.225	-	-1.2668	1.4721	-1.42	-1.2757	-1.92	-	1.128	1.225	
	Toliana Madagascar	2	28.00	15.009	11	26.00	41	-	-	-	-	-1.4397	3.9029	-2.80	-1.4397	-1.88	-	-	-	
	Total	115	26.52	1.788	11	18.00	169	4.841	447	2.118	226	-1.4288	0.4728	-2.80	-1.6032	-1.08	-2.54	447	2.91	226
Goniastrea	Arabavakolia Madagascar	51	14.32	1.224	11	14.00	52	3.220	456	1.617	333	-1.6524	0.4946	-2.80	-1.6996	-1.67	-3.528	456	2.758	333
	Famusa Banksi Sraak Arabia	435	17.54	.310	11	13.00	49	3.048	224	1.825	312	-1.6783	0.1331	-2.80	-1.7447	-1.72	-0.448	224	2.80	312
	Gracilaria Seychelles	431	22.69	.617	11	18.00	100	6.810	235	2.049	118	-1.6977	0.1999	-2.80	-1.9021	-1.10	-1.108	235	2.63	118
	Total	919	18.60	1.150	15	13.50	65	-4.25	1.232	541	6.37	-1.1760	1.3465	-1.89	-1.6028	-1.40	-1.071	1.232	-2.53	637
Goniopora	Arabavakolia Madagascar	27	31.06	3.425	11	24.00	67	-5.62	1.72	644	4.48	-1.2833	0.9781	-2.80	-1.3468	-1.43	-1.477	672	1.38	448
	Famusa Banksi Sraak Arabia	183	22.16	1.375	11	18.00	73	4.329	472	1.905	238	-1.3337	0.3924	-2.80	-1.6021	-1.38	-2.27	472	2.68	238
	Gracilaria Seychelles	178	26.84	1.351	11	20.00	133	7.888	342	2.172	182	-1.3428	0.3586	-2.80	-1.5086	1.14	-3.25	342	6.81	182
	Total	390	23.58	1.600	11	19.00	133	6.813	276	2.095	138	-1.4232	0.2618	-2.80	-1.5528	1.14	-3.54	276	6.77	138
Gyrostelia	Famusa Banksi Sraak Arabia	6	12.67	.815	11	13.00	15	-1.164	1.741	3.13	845	-1.9885	0.5980	-2.80	-1.8860	-1.74	2.626	1.741	645	845
	Total	6	12.67	.815	11	13.00	15	-1.164	1.741	3.13	845	-1.9885	0.5980	-2.80	-1.8860	-1.74	2.626	1.741	645	845
Halysites	Arabavakolia Madagascar	1	29.00	-	29	29.00	29	-	-	-	-	-1.1885	-	-1.18	-1.1800	-1.18	-	-	-	-
	Total	1	29.00	-	29	29.00	29	-	-	-	-	-1.1885	-	-1.18	-1.1800	-1.18	-	-	-	-
Harpolitha	Arabavakolia Madagascar	5	18.20	2.154	12	18.00	25	-4.78	2.068	264	8.13	-1.6156	0.9718	-1.84	-1.9021	-1.31	2.626	2.068	-3.34	813
	Famusa Banksi Sraak Arabia	36	21.44	.843	13	22.50	33	-7.22	2.68	163	393	-1.4680	0.3573	-1.89	-1.3985	-1.07	-2.788	2.68	-2.55	393
	Gracilaria Seychelles	5	43.20	4.880	24	43.00	51	1.454	2.069	-1.235	913	-1.9048	0.1810	-1.35	-3.386	-1.69	2.835	2.069	-1.590	913
	Total	46	23.24	1.283	12	23.00	51	3.852	888	1.618	350	-1.4224	0.4220	-1.84	-1.7398	-1.65	2.808	888	3.78	350
Hydaphara	Arabavakolia Madagascar	36	21.77	1.611	11	19.00	42	-0.60	835	877	427	-1.4981	0.6190	-2.80	-1.5528	-1.86	-8.78	835	274	427
	Famusa Banksi Sraak Arabia	37	36.08	4.735	11	27.00	152	6.774	359	2.376	388	-1.1881	0.9023	-2.80	-1.2440	2.6	1.42	359	625	388
	Gracilaria Seychelles	59	19.92	1.386	11	17.00	48	1.890	341	1.307	378	-1.5754	0.3586	-2.80	-1.6380	-1.80	-4.071	341	678	378
	Total	7	16.29	1.911	11	15.00	23	-1.951	1.587	318	394	-1.7115	0.9080	-2.80	-1.7447	-1.38	-2.052	1.587	1.62	394
Leptastrea	Arabavakolia Madagascar	42	17.52	1.236	11	13.00	42	3.409	317	2.038	365	-1.6833	0.4941	-2.80	-1.7447	-1.96	1.241	317	1.410	365
	Famusa Banksi Sraak Arabia	188	14.11	.405	11	12.00	58	9.562	461	2.905	233	-1.8382	0.2138	-2.80	-1.9588	-1.95	4.431	461	2.065	233
	Gracilaria Seychelles	135	20.57	1.710	11	18.00	51	1.514	414	1.197	209	-1.5421	0.2786	-2.80	-1.9021	-1.69	-6.78	414	4.06	209
	Toliana Madagascar	10	23.60	1.280	13	19.50	42	-1.040	1.334	685	687	-1.4336	0.1781	-1.89	-1.5360	-1.86	-1.591	1.334	348	687
	Total	285	17.87	.496	11	13.00	51	2.414	265	1.619	142	-1.6889	0.3573	-2.80	-1.7447	-1.69	-1.088	265	0.53	142
Leptaria	Arabavakolia Madagascar	4	26.73	4.629	14	18.50	32	1.215	2.619	1.296	1.614	-1.5189	0.9080	-1.82	-1.5779	-1.10	-3.53	2.619	253	1.614
	Famusa Banksi Sraak Arabia	2	16.50	3.480	13	16.50	20	-	-	-	-	-1.6673	1.6071	-1.89	-1.6973	-1.51	-	-	-	-
	Gracilaria Seychelles	3	30.67	8.782	17	28.00	47	-	-	794	1.225	-1.2026	2.5299	-1.84	-1.2078	-1.76	-	0.03	1.225	
	Total	10	38.10	8.386	15	33.50	67	-1.981	1.334	323	897	-1.0626	1.5066	-1.74	-1.0377	-1.45	-1.742	1.334	-0.91	897
Leptoseris	Arabavakolia Madagascar	19	31.06	4.672	13	24.00	67	-4.17	1.014	944	524	-1.2476	0.9817	-1.89	-1.3468	-1.45	-1.198	1.014	404	524
	Famusa Banksi Sraak Arabia	16	18.60	2.325	12	15.50	48	4.391	1.061	2.369	564	-1.6378	0.8444	-1.86	-1.7218	-1.74	1.851	1.061	1.452	564
	Total	57	15.98	.792	11	14.00	42	6.845	823	2.409	316	-1.7419	0.3439	-2.80	-1.8238	-1.86	2.213	823	1.424	316
Leptoseris	Gracilaria Seychelles	2	11.00	.000	11	11.00	11	-	-	-	-	-2.0000	0.0000	-2.80	-2.0000	-2.80	-	-	-	-
	Total	79	16.43	.789	11	14.00	48	7.830	848	2.564	277	-1.7366	0.3714	-2.80	-1.8238	-1.74	2.285	848	1.489	277

**(Table 12
continued)**

Genus	Region	N	Maximum colony diameter (cm)									Logarithmically transformed colony surface area								
			Mean	Std. Error of Mean	Minimum	Median	Maximum	Kurtosis	Std. Error of Kurtosis	Skewness	Std. Error of Skewness	Mean	Std. Error of Mean	Minimum	Median	Maximum	Kurtosis	Std. Error of Kurtosis	Skewness	Std. Error of Skewness
Lobophylla	Andrevolanka Madagascar	11	14.60	.375	11	13.00	19	-.395	1.279	.822	.661	-1.8294	.04850	-2.00	-1.5881	-1.55	-1.044	1.279	.664	.661
	Farasan Banks Saudi Arabia	137	25.79	2.031	11	20.00	225	37.905	431	5.270	297	-1.4455	.07986	-2.00	-1.5699	.60	2.648	431	1.338	297
	Croazie Seychelles	39	18.65	4.863	11	28.00	131	2.763	741	1.717	.378	-1.1614	.09008	-2.00	-1.2659	.33	-.696	741	468	378
	Tolima Madagascar	3	11.90	-	11	11.00	11	-	-	-	-	-2.0000	-	-2.00	-2.0000	-2.00	-	-	-	-
	Total	188	23.55	1.833	11	19.90	225	23.083	353	4.029	177	-1.4120	.07219	-2.00	-1.5387	.60	3.322	353	1.154	177
Meridia	Andrevolanka Madagascar	8	27.24	6.806	11	22.00	67	1.773	1.481	1.357	.752	-1.4012	.26300	-2.00	-1.4626	-.45	-0.218	1.481	463	.752
	Farasan Banks Saudi Arabia	27	17.44	1.153	11	15.00	35	1.585	.832	1.394	.448	-1.6656	.05120	-2.00	-1.7447	-1.02	-.933	.832	833	.448
	Croazie Seychelles	3	22.66	-	22	22.00	22	-	-	-	-	-1.4202	-	-1.42	-1.4202	-1.42	-	-	-	-
	Tolima Madagascar	36	18.78	1.813	11	15.50	67	9.424	.788	2.876	.393	-1.8603	.09350	-2.00	-1.7218	-.45	0.288	.788	1.212	.393
	Total	74	23.46	4.000	19	23.00	27	-	-	-	-	-1.3985	.15436	-1.55	-1.3985	-1.24	-	-	-	-
Miliopora	Andrevolanka Madagascar	2	23.46	4.000	19	23.00	27	-	-	-	-	-1.3985	.15436	-1.55	-1.3985	-1.24	-	-	-	-
	Farasan Banks Saudi Arabia	134	15.84	1.894	11	30.00	159	5.878	418	1.912	.289	-1.1311	.04158	-2.00	-1.1487	.25	-.308	418	.159	.289
	Croazie Seychelles	41	18.20	6.808	11	24.00	275	23.147	324	4.397	.369	-1.2660	.09717	-2.00	-1.3488	.37	1.487	324	1.048	.369
	Tolima Madagascar	8	16.83	4.331	28	37.50	49	-.344	1.741	-.596	.845	-1.9091	.11678	-1.51	-.8587	-.72	1.288	1.741	-1.149	.845
	Total	183	15.83	2.032	11	30.00	275	31.094	357	4.298	180	-1.1602	.07779	-2.00	-1.1487	.37	2.35	357	4.04	180
Montanea	Andrevolanka Madagascar	14	23.93	3.992	11	20.00	58	1.298	1.124	1.418	.597	-1.4797	.12839	-2.00	-1.4894	-.38	-.837	1.124	.837	.597
	Farasan Banks Saudi Arabia	11	28.91	4.440	12	20.00	52	-1.348	1.279	.641	.661	-1.3674	.14395	-1.96	-1.5086	-.67	-1.886	1.279	278	.661
	Croazie Seychelles	110	18.98	.683	11	17.00	49	2.743	457	1.547	.230	-1.6056	.02809	-2.00	-1.6383	-.32	-.840	457	.686	.230
	Tolima Madagascar	4	18.59	9.665	11	44.00	55	2.117	2.619	-1.425	1.814	-1.0963	.31832	-2.00	-.8210	-.82	3.358	2.619	-1.812	1.814
	Total	139	20.68	8.59	11	17.00	58	2.790	488	1.728	.206	-1.5385	.09333	-2.00	-1.6383	-.58	-.845	488	845	.206
Montipora	Andrevolanka Madagascar	189	24.24	1.022	11	21.00	111	14.413	243	3.227	172	-1.4219	.02303	-2.00	-1.4559	-.81	0.322	343	928	172
	Farasan Banks Saudi Arabia	147	23.48	.553	11	19.00	145	13.850	281	2.563	101	-1.4692	.09887	-2.00	-1.5528	.22	-.151	281	668	101
	Croazie Seychelles	76	27.68	2.581	11	19.90	149	11.791	345	3.124	.276	-1.4168	.09790	-2.00	-1.5387	.19	.921	345	1.009	.276
	Tolima Madagascar	31	23.32	2.549	11	20.00	64	2.960	.821	1.644	.821	-1.4771	.03823	-2.00	-1.5086	-.49	-.372	.821	375	.821
	Total	483	24.61	4.89	11	19.00	145	15.789	163	3.037	.082	-1.4542	.03780	-2.00	-1.5528	.22	-.356	343	739	.082
Myceium	Andrevolanka Madagascar	15	22.87	3.633	11	16.00	42	-.370	1.123	1.057	.580	-1.5214	.12900	-2.00	-1.6080	-.57	-1.150	1.123	678	.580
	Farasan Banks Saudi Arabia	22	31.77	4.298	11	28.00	90	1.988	.593	1.364	.491	-1.2537	.11190	-2.00	-1.1940	-.20	-.834	.593	.188	.491
	Croazie Seychelles	2	32.68	13.800	19	32.00	45	-	-	-	-	-1.1757	.37312	-1.55	-1.1757	-.80	-	-	-	-
	Tolima Madagascar	39	28.36	2.886	11	23.00	90	2.173	.741	1.380	.378	-1.3527	.06237	-2.00	-1.3768	-.20	-1.629	.741	328	.378
	Total	78	28.68	4.89	11	23.00	90	2.173	.741	1.380	.378	-1.3527	.06237	-2.00	-1.3768	-.20	-1.629	.741	328	.378
Oculophylla	Andrevolanka Madagascar	3	35.68	-	33	35.00	35	-	-	-	-	-1.9177	-	-1.82	-1.0177	-1.02	-	-	-	
	Farasan Banks Saudi Arabia	10	24.38	2.692	18	23.00	45	3.838	1.334	1.696	.687	-1.3736	.08818	-1.70	-1.3788	-.80	1.131	1.334	.736	.687
	Croazie Seychelles	3	28.00	-	28	20.00	20	-	-	-	-	-1.5086	-	-1.51	-1.5086	-1.51	-	-	-	-
	Tolima Madagascar	3	15.68	-	15	15.00	15	-	-	-	-	-1.7447	-	-1.74	-1.7447	-1.74	-	-	-	-
	Total	19	24.68	2.563	15	23.00	45	1.944	1.191	1.828	.636	-1.3852	.07801	-1.74	-1.3788	-.80	.097	1.191	.596	.636
Ocyrops	Andrevolanka Madagascar	3	18.71	2.032	11	17.00	28	.834	1.583	.688	.794	-1.5859	.09348	-2.00	-1.6383	-1.21	1.078	1.583	-.326	.794
	Farasan Banks Saudi Arabia	11	18.73	1.879	12	18.00	33	1.673	1.279	1.357	.661	-1.6643	.09057	-1.96	-1.6621	-1.07	1.46	1.279	.777	.661
	Tolima Madagascar	3	14.00	-	14	14.00	14	-	-	-	-	-1.8259	-	-1.82	-1.8259	-1.82	-	-	-	-
	Total	19	18.47	1.905	11	17.00	33	1.697	1.014	1.153	.524	-1.6091	.09751	-2.00	-1.6383	-1.07	-.099	1.014	.548	.524
	Packysoria	Andrevolanka Madagascar	96	28.43	2.032	11	19.00	99	1.434	488	1.418	.246	-1.3723	.05423	-2.00	-1.3528	-.31	-.885	488	821
Farasan Banks Saudi Arabia		2	18.68	2.000	17	19.00	21	-	-	-	-	-1.5471	.09117	-1.84	-1.5471	-1.46	-	-	-	-
Croazie Seychelles		3	13.68	-	13	13.00	13	-	-	-	-	-1.8961	-	-1.89	-1.8961	-1.89	-	-	-	-
Total		99	28.68	1.981	11	19.00	99	1.393	481	1.467	.283	-1.3812	.05792	-2.00	-1.3528	-.31	-.818	481	858	.283
Parona		Andrevolanka Madagascar	88	28.78	2.676	11	16.00	249	68.609	548	7.862	.297	-1.8247	.04348	-2.00	-1.6690	.66	10.561	548	2.441
	Farasan Banks Saudi Arabia	315	18.67	.583	11	16.00	114	25.497	268	3.451	.133	-1.6287	.09337	-2.00	-1.6690	.60	3.422	268	1.129	.133
	Croazie Seychelles	194	28.51	.838	11	16.00	72	4.723	347	2.083	.175	-1.5989	.02863	-2.00	-1.6990	-.39	.292	347	1.024	.175
	Tolima Madagascar	19	18.11	1.642	11	14.00	40	6.588	1.014	2.428	.524	-1.7516	.08823	-2.00	-1.8239	-.90	2.591	1.014	1.714	.524
	Total	626	18.66	.593	11	16.00	249	105.170	184	7.731	.097	-1.6190	.06487	-2.00	-1.6690	.66	2.643	394	1.340	.097
Physogera	Andrevolanka Madagascar	3	23.33	10.888	11	14.00	45	1.863	1.863	1.225	.580	-1.5488	.37458	-2.00	-1.8239	-.80	-	-	-	
	Farasan Banks Saudi Arabia	15	18.33	2.324	11	15.00	38	.281	1.121	1.158	.580	-1.6487	.09709	-2.00	-1.7447	-.85	-.882	1.121	.728	.580
	Croazie Seychelles	12	48.59	9.243	15	32.00	110	-.821	1.232	.773	.637	-.5889	.17966	-1.74	-1.1115	-.82	-1.643	1.232	.188	.637
	Total	30	38.28	4.611	11	20.90	110	2.711	823	1.778	.427	-1.3652	.08847	-2.00	-1.4923	-.82	-.451	823	.788	.427
	Physogera	Andrevolanka Madagascar	46	22.21	2.216	11	16.00	81	5.524	.874	2.386	.343	-1.5451	.06772	-2.00	-1.6686	-.29	.979	.874	1.234
Farasan Banks Saudi Arabia		175	23.64	.599	11	19.00	92	7.573	.385	2.366	.184	-1.4826	.09811	-2.00	-1.5528	-.38	.319	.385	.805	.184
Croazie Seychelles		51	18.94	1.464	11	15.00	66	8.458	.656	2.586	.333	-1.6394	.09996	-2.00	-1.7447	-.47	3.215	.656	1.226	.333
Tolima Madagascar		22	18.82	1.988	11	15.50	48	3.995	.853	1.955	.491	-1.8320	.05460	-2.00	-1.7218	-.34	.720	.853	1.095	.491
Total		294	21.88	.753	11	17.00	92	7.347	.282	2.412	.142	-1.5308	.02325	-2.00	-1.6383	-.38	.497	.282	.953	.142

(Table 12 continued)

Genus	Region	N	Maximum colony diameter (cm)									Logarithmically transformed colony surface area								
			Mean	Std. Error of Mean	Minimum	Median	Maximum	Kurtosis	Std. Error of Kurtosis	Skewness	Std. Error of Skewness	Mean	Std. Error of Mean	Minimum	Median	Maximum	Kurtosis	Std. Error of Kurtosis	Skewness	Std. Error of Skewness
Phragmites	Andorradonka Madunacac	7	23.14	12.483	18	41.00	98	-3.782	1.587	-.529	-.794	-0.115	21.788	-1.00	-0.794	-12	-1.717	1.587	.011	.794
	Finnson Banko Saadi Anbiha	15	22.27	7.828	12	18.00	58	8.853	1.121	2.218	.589	-0.4924	89550	-1.90	-0.6621	-58	1.118	1.121	1.828	.588
	Total	22	22.06	8.267	12	23.83	58	2.462	.837	1.838	.481	-0.7787	11831	-1.36	-0.5608	-12	-0.812	.983	.982	.207
Plectonera	Andorradonka Madunacac	4	19.00	1.581	16	18.50	23	-0.768	2.609	.672	1.034	-0.5157	87184	-1.70	-0.5755	-18	-0.691	2.615	.527	1.034
	Finnson Banko Saadi Anbiha	7	28.29	8.198	11	13.00	57	8.431	1.587	2.311	.794	-0.8435	18371	-2.00	-0.8801	-59	4.982	1.587	2.175	.794
	Genetika Sevebelin	8	53.11	8.799	14	25.00	78	-1.87	1.480	1.803	.717	-0.2085	10954	-1.82	-0.5898	-41	-0.854	1.408	3.84	.717
Total	20	25.86	3.811	11	19.80	78	3.538	.992	1.874	.517	-0.4245	10786	-2.00	-0.5387	-41	-0.888	.992	.976	.512	
Pachyera	Andorradonka Madunacac	206	15.46	3.86	11	17.00	54	3.775	.378	1.844	.169	-0.8487	81452	-2.00	-0.6363	-93	-0.385	.378	3.49	.169
	Finnson Banko Saadi Anbiha	481	28.43	5.96	11	27.00	85	2.86	.232	1.322	.111	-0.2482	81529	-2.00	-0.2441	-28	-0.241	.232	-0.897	.111
	Genetika Sevebelin	787	23.04	3.90	11	18.00	101	10.854	.384	2.313	.092	-0.5783	81310	-2.00	-0.6821	-10	.406	.184	.794	.092
Total Madunacac	26	17.23	1.819	11	15.80	38	-0.94	.887	.799	.456	-0.4678	80884	-2.00	-0.4714	-12	-0.878	.887	4.99	.456	
Total	1472	22.97	2.85	11	20.00	181	3.798	.378	1.874	.685	-0.8671	80949	-2.00	-0.5886	-10	-0.227	.178	.880	.685	
Podakaria	Andorradonka Madunacac	2	24.00	11.808	12	24.00	35	-	-	-	-	-0.4019	45416	-1.89	-0.4019	-182	-	-	-	-
	Finnson Banko Saadi Anbiha	2	23.50	3.588	16	21.89	27	-	-	-	-	-0.4715	22742	-1.70	-0.4715	-124	-	-	-	-
	Total	4	23.75	5.872	13	21.82	33	-2.813	2.609	-.875	1.034	-0.8817	20877	-1.89	-0.4714	-182	-0.548	2.815	.084	1.034
Purkin	Andorradonka Madunacac	283	38.21	1.934	11	20.00	387	27.464	2.69	4.818	.145	-0.9628	85185	-2.00	-0.5886	.87	2.286	2.69	1.545	.145
	Finnson Banko Saadi Anbiha	3718	25.12	3.86	11	20.00	290	95.523	.880	5.213	.845	-0.4784	89389	-2.00	-0.5886	.87	.908	.985	.880	.845
	Genetika Sevebelin	1484	38.21	1.124	11	25.00	525	20.898	.327	4.824	.084	-0.1954	81644	-2.00	-0.5886	1.38	.286	1.27	.845	.084
Total	41	23.12	2.548	11	18.00	98	8.728	.724	2.493	.389	-0.5046	87621	-2.00	-0.6821	-29	.888	.724	.882	.389	
Pannocera	Andorradonka Madunacac	5124	38.47	4.67	11	21.00	621	98.427	.888	5.883	.674	-0.3982	88738	-2.00	-0.4959	1.38	1.480	.988	1.111	.674
	Andorradonka Madunacac	32	23.53	3.773	11	17.00	114	16.518	.808	3.888	.414	-0.5477	88732	-2.00	-0.6363	.01	2.682	.808	1.888	.414
	Finnson Banko Saadi Anbiha	23	18.04	2.588	11	14.00	60	6.778	.876	2.478	.481	-0.7045	88284	-2.00	-0.8278	-55	3.487	.935	1.985	.481
Genetika Sevebelin	14	18.78	3.288	11	15.00	55	8.817	1.154	3.505	.587	-0.8622	88885	-2.00	-0.7447	-62	2.680	1.154	1.888	.587	
Total Madunacac	70	13.08	-	11	11.89	11	-	-	-	-	-2.8880	-	-2.00	-2.0000	-2.80	-	-	-	-	
Total	70	28.86	2.832	11	15.00	114	13.882	.586	3.379	.287	-0.8288	88312	-2.00	-0.7447	.01	2.678	.586	1.755	.287	
Scribneria	Andorradonka Madunacac	18	28.29	1.542	11	18.00	58	1.213	1.088	1.584	.336	-0.4848	10952	-2.00	-0.6621	-58	.878	1.808	.981	.336
	Finnson Banko Saadi Anbiha	107	24.45	1.857	11	22.00	63	3.287	.460	1.286	.238	-0.4854	88984	-2.00	-0.4382	-53	-0.888	.863	.284	.238
	Genetika Sevebelin	8	28.00	-	20	20.00	28	-	-	-	-	-0.5886	-	-1.51	-0.5886	-1.51	-	-	-	-
Total	126	24.38	1.824	11	21.89	63	3.368	.428	1.316	.216	-0.4135	88318	-2.00	-0.4381	-53	-0.882	.863	.284	.216	
Sideraster	Andorradonka Madunacac	1	25.00	-	25	25.00	25	-	-	-	-	-0.3888	-	-1.31	-0.3888	-1.31	-	-	-	-
	Total	1	25.00	-	25	25.00	25	-	-	-	-	-0.3888	-	-1.31	-0.3888	-1.31	-	-	-	-
	Finnson Banko Saadi Anbiha	3	28.57	2.734	11	17.00	33	-0.669	1.587	-.835	.784	-0.5980	15386	-2.00	-0.6363	-97	-0.381	1.587	.882	.784
Total	3	28.57	2.734	11	17.00	33	-0.669	1.587	-.835	.784	-0.5980	15386	-2.00	-0.6363	-97	-0.381	1.587	.882	.784	
Stylocystidia	Andorradonka Madunacac	59	13.34	1.864	11	13.00	88	17.828	.813	4.282	.311	-0.7456	88177	-2.00	-0.8861	-24	9.587	.813	2.988	.311
	Finnson Banko Saadi Anbiha	153	22.19	7.29	11	20.00	58	7.32	.388	1.887	.186	-0.4784	82897	-2.00	-0.5886	-71	-0.388	.388	.283	.186
	Genetika Sevebelin	289	15.46	3.84	11	14.00	34	1.488	.335	1.286	.188	-0.7480	81533	-2.00	-0.8278	-1.88	-0.231	.335	.799	.188
Total	421	18.24	4.27	11	16.00	88	17.882	.237	3.278	.119	-0.6582	81542	-2.00	-0.6988	-24	1.686	.237	1.172	.119	
Synophelia	Finnson Banko Saadi Anbiha	48	13.13	.957	11	13.50	34	.886	.338	1.388	.234	-0.8188	88227	-2.00	-0.7218	-1.84	-0.428	.733	.821	.234
	Genetika Sevebelin	1	13.00	-	13	13.00	13	-	-	-	-	-0.8861	-	-1.89	-0.8861	-1.89	-	-	-	-
	Total Madunacac	1	13.08	-	11	11.89	11	-	-	-	-	-2.8880	-	-2.00	-2.0000	-2.80	-	-	-	-
Total	42	18.88	.889	11	15.00	34	.932	.317	1.297	.385	-0.4914	88123	-2.00	-0.7447	-1.88	-0.387	.717	.882	.385	
Trachypeltia	Finnson Banko Saadi Anbiha	2	21.56	2.588	18	21.89	25	-	-	-	-	-0.4559	14813	-1.48	-0.4559	-1.31	-	-	-	-
	Total	2	21.56	2.588	18	21.89	25	-	-	-	-	-0.4559	14813	-1.48	-0.4559	-1.31	-	-	-	-
	Andorradonka Madunacac	8	28.33	3.188	12	19.00	33	-0.617	1.781	-.883	.845	-0.5420	11548	-1.98	-0.5471	-1.87	-0.886	1.781	.211	.845
Turbinaria	Finnson Banko Saadi Anbiha	31	13.52	1.286	11	16.00	45	6.192	.828	2.288	.421	-0.8781	85214	-2.00	-0.6988	-88	1.483	.821	1.189	.421
	Genetika Sevebelin	80	28.18	3.388	11	22.50	128	13.827	.338	3.828	.378	-0.3878	87555	-2.00	-0.3885	.12	.881	.733	.882	.378
	Total	77	23.23	1.862	11	18.00	128	26.885	.548	3.888	.238	-0.8881	88841	-2.00	-0.6821	-12	1.790	.541	1.188	.238
Ulnocoma	Andorradonka Madunacac	1	98.00	-	88	88.00	99	-	-	-	-	-1.8881	-	-1.31	-1.8881	-1.31	-	-	-	-
	Finnson Banko Saadi Anbiha	3	13.00	1.528	11	12.00	18	-	-	1.458	1.225	-0.8859	89421	-2.00	-0.9586	-1.30	-	-	1.607	1.225
	Genetika Sevebelin	5	15.00	2.787	11	11.88	25	3.335	2.080	1.838	.813	-0.7886	11891	-2.00	-0.8886	-1.31	-0.823	2.888	1.186	.813
Total	8	23.06	8.883	11	12.00	99	8.213	1.480	2.835	.717	-0.4415	38865	-2.00	-0.9586	-1.31	5.223	1.480	2.228	.717	
Total	Andorradonka Madunacac	2358	24.64	4.75	11	18.00	388	71.513	.388	6.754	.689	-0.4785	89854	-2.00	-0.6821	1.87	2.789	.181	1.385	.689
	Finnson Banko Saadi Anbiha	8742	23.86	1.89	11	19.00	388	48.898	.852	4.838	.826	-0.4787	89448	-2.00	-0.5528	.83	.793	.882	.828	.828
	Genetika Sevebelin	7377	28.82	2.88	11	19.00	523	78.827	.858	6.478	.829	-0.4781	89985	-2.00	-0.5528	1.34	1.711	.858	1.222	.828
Total Madunacac	412	22.88	.732	11	18.00	98	3.339	.248	1.828	.129	-0.3155	88280	-2.00	-0.6821	-28	-0.281	.248	.828	.129	
Total	18898	24.97	1.96	11	19.00	523	87.878	.858	6.703	.808	-0.4789	89332	-2.00	-0.5528	1.34	1.673	.858	1.141	.818	

Appendix IV: Univariate testing of coral size per genus

Table 13. Mean colony size (surface area, m²) of region-specific populations of all genera, based on all colonies >10cm maximum diameter, showing standard deviation, sample size and significance of between-region differences (excluding Toliara) from ANOVA testing

Genus	Andavadoaka Madagascar			Farasan Banks Saudi Arabia			Granitic Seychelles			ANOVA <i>P</i>
	<i>n</i>	<i>mean</i>	<i>SD</i>	<i>n</i>	<i>mean</i>	<i>SD</i>	<i>n</i>	<i>mean</i>	<i>SD</i>	
Acropora	427	0.05896	0.10472	459	0.1136	0.2823	1362	0.12265	0.24682	< 0.000
Acanthastrea	17	0.02735	0.01509	44	0.02057	0.01408	106	0.03134	0.02737	0.021
alveopora	0	0	0	1	0.01	0	5	0.0704	0.0668	
Astreopora	44	0.0846	0.1161	51	0.0675	0.099	54	0.0978	0.2272	0.866
Blastomussa	0	0	0	13	0.02485	0.02097	5	0.0324	0.0188	
Coscinarea	25	0.01876	0.01373	21	0.0451	0.0697	7	0.01714	0.01049	0.241
Ctenactis	0	0	0	43	0.03949	0.02179	0	0	0	
Cyphastrea	18	0.03389	0.03213	67	0.02282	0.01665	47	0.03168	0.04676	0.819
Diploastrea	9	3.04	3.68	44	0.2876	0.5801	20	1.418	3.994	0.008
Echinophyllia	13	0.0562	0.048	28	0.0394	0.0919	0	0	0	
Echinopora	123	0.2731	0.9476	727	0.04847	0.06117	35	0.0599	0.0852	< 0.000
Favia	138	0.04286	0.05932	245	0.0465	0.1851	510	0.0305	0.08716	< 0.000
Favites	96	0.03592	0.06364	53	0.03068	0.03404	1094	0.030649	0.02936	0.38
Fungia	20	0.0155	0.01053	46	0.015261	0.006351	61	0.0308	0.1433	0.026
Galaxea	107	0.02336	0.0213	319	0.01896	0.02059	79	0.0478	0.114	< 0.000
Gardineroseris	33	0.1798	0.2402	77	0.04242	0.04273	3	0.07	0.0431	
Goniastrea	51	0.03237	0.03558	475	0.02768	0.02505	431	0.05326	0.07611	< 0.000
Goniopora	27	0.0994	0.1034	103	0.0495	0.06387	178	0.0819	0.1408	0.04
Gyrosmlia	0	0	0	6	0.01283	0.00293	0	0	0	
Halomitra	1	0.066	0	0	0	0	0	0	0	
Herpolitha	5	0.0272	0.01422	36	0.038	0.01755	5	0.1404	0.0632	
Hydnophora	30	0.04303	0.03589	37	0.1656	0.3263	39	0.03685	0.03501	0.002
Leptastrea	42	0.02902	0.03233	108	0.01748	0.01621	135	0.03845	0.03383	< 0.000
Leptoria	4	0.0375	0.0296	2	0.022	0.01273	3	0.086	0.0778	
Leptoseris	16	0.0336	0.0423	57	0.02277	0.02207	2	0.01	0	
Lobophyllia	11	0.01573	0.00602	137	0.0962	0.3588	39	0.1824	0.307	
Merulina	8	0.0844	0.1157	27	0.02652	0.02032	1	0.038		
Millepora	2	0.0425	0.0205	134	0.138	0.2071	41	0.248	0.925	
Montastrea	14	0.0612	0.079	11	0.0722	0.072	110	0.03215	0.02861	0.3
montipora	199	0.06348	0.1148	587	0.05735	0.09528	76	0.0965	0.2288	0.192
Mycedium	15	0.0555	0.0655	22	0.1096	0.1454	2	0.0935	0.0926	
Oulophyllia	1	0.096		10	0.0516	0.0406	1	0.031		
Oxypora	7	0.02971	0.01703	11	0.03009	0.02218	0	0	0	
Pachyseris	96	0.0942	0.137	2	0.029	0.00849	1	0.013		
Pavona	88	0.0828	0.4804	335	0.03749	0.07337	194	0.04414	0.06392	0.58
Physogyra	3	0.0613	0.0846	15	0.03293	0.03283	12	0.2438	0.2929	
Platygyra	48	0.0568	0.0981	175	0.05522	0.08394	51	0.03651	0.05462	0.019
Plesiastrea	4	0.029	0.00983	7	0.0503	0.0905	9	0.1149	0.134	
Pocillopora	208	0.025361	0.013935	481	0.07314	0.06296	707	0.04319	0.0593	< 0.000
Podabacia	2	0.0545	0.0587	2	0.0385	0.0262	0	0	0	
Porities	283	1.4719	0.198	3316	1.495	0.1695	1485	1.412	0.2305	< 0.000
Psammocora	32	0.0781	0.1896	23	0.0372	0.0657	14	0.0383	0.061	0.32
Seriatopora	18	0.0631	0.0833	107	0.05621	0.05443	0	0	0	
Siderastrea	1	0.049	0	0	0	0	0	0	0	
Stylocoeniella	0	0	0	7	0.04	0.0371	0	0	0	
Stylopora	59	0.0394	0.1064	153	0.04499	0.03888	210	0.020548	0.012833	< 0.000
Symphyllia	0	0	0	40	0.02565	0.01873	1	0.013	0	
Turbinarea	6	0.0365	0.0279	31	0.02803	0.02904	40	0.0959	0.209	

Key	
bold	Significant variation in coral size (surface area) (ANOVA $p \leq 0.05$)
	Unable to perform ANOVA due to data supporting insufficient power
	Unable to perform ANOVA due to lack of data within one or more regions

Table 14. Mean colony size (surface area, m²) of populations of all genera within the Farsan Banks, Saudi Arabia, subdivided by degree of observed mortality, based on all colonies >10cm maximum diameter, showing standard deviation, sample size and significance of between-group differences from two-sample T-test

Genus	Farasan Banks: sites with no recorded mortality			Farasan Banks: sites with moderate or high mortality			2 sample t-test
	<i>n</i>	<i>mean</i>	<i>SD</i>	<i>n</i>	<i>mean</i>	<i>SD</i>	<i>P</i>
Acanthastrea	37	0.02205	0.01478	5	0.01271	0.00489	0.046
Acropora	366	0.1213	0.3126	93	0.08316	0.08786	0.760
Alveopora	1	0.01					
Astreopora	28	0.0747	0.0883	23	0.0588	0.1137	0.156
Blastomussa	5	0.0318	0.0309	8	0.0205	0.01234	0.551
Coscinarea	20	0.0463	0.0714	1	0.023		
Ctenactis	16	0.04819	0.0222	27	0.03433	0.02021	0.039
Cyphastrea	51	0.0249	0.01845	16	0.01619	0.00476	0.032
Diploastrea	35	0.299	0.621	9	0.244	0.407	0.777
Echinophyllia	22	0.0468	0.1029	6	0.01233	0.00294	0.001
Echinopora	610	0.04985	0.05961	117	0.04129	0.06854	0.000
Favia	180	0.0544	0.2153	65	0.02448	0.01824	0.031
Favites	44	0.03189	0.03601	9	0.02478	0.02271	0.441
Fungia	35	0.01606	0.00699	11	0.012727	0.002494	0.144
Galaxea	195	0.018036	0.009953	124	0.02041	0.03059	0.507
Gardineroseris	48	0.04506	0.04302	29	0.03803	0.04263	0.273
Goniastrea	357	0.02923	0.02718	118	0.02301	0.01628	0.046
Goniopora	61	0.05411	0.07218	42	0.04281	0.04947	0.449
Gyrosmlia	5	0.0128	0.00327	1	0.013		
Herpolitha	12	0.03092	0.01302	24	0.04154	0.01867	0.083
Hydnophora	29	0.1726	0.3611	8	0.1404	0.1578	0.920
Leptastrea	85	0.01749	0.01603	23	0.01743	0.01722	0.911
Leptoria	2	0.022	0.01273				
Leptoseris	41	0.0242	0.02462	16	0.01913	0.01351	0.609
Lobophyllia	100	0.1104	0.4111	37	0.0579	0.1397	0.086
Merulina	27	0.02652	0.02032				
Millepora	68	0.1128	0.1038	66	0.1638	0.2744	0.867
Montastrea	9	0.0848	0.0741	2	0.0155	0.00636	
Montipora	440	0.06408	0.10611	147	0.03718	0.04506	0.000
Mycidium	20	0.0882	0.0883	2	0.324	0.442	
Oulophyllia	10	0.0516	0.0406				
Oxypora	9	0.03333	0.02334	2	0.0155	0.00636	
Pachyseris	2	0.029	0.00849				
Pavona	295	0.03492	0.06653	40	0.0564	0.111	0.437
Physogyra	13	0.02554	0.02534	2	0.081	0.0453	
Platygyra	111	0.06657	0.09976	64	0.03555	0.03824	0.004
Plerogyra	14	0.05	0.0654	1	0.035		
Plesiastrea	3	0.0937	0.1397	4	0.01775	0.00802	0.711
Pocillopora	252	0.06929	0.06266	229	0.07738	0.06315	0.023
Podabacia	2	0.0385	0.0262				
Porites	2202	0.08072	0.24029	1114	0.06148	0.24247	0.000
Psammocora	16	0.0465	0.0775	7	0.01586	0.00767	0.267
Seriatopora	86	0.05865	0.05665	21	0.04624	0.04396	0.450
Stylocoeniella	4	0.061	0.037	3	0.012	0.00265	0.007
Stylophora	131	0.04651	0.04096	22	0.03595	0.02144	0.492
Symphyllia	34	0.02591	0.01834	6	0.02417	0.02266	0.442
Turbinarea	13	0.0366	0.041	18	0.02183	0.01423	0.579

Key	
bold	Significant variation in coral size (surface area) (two-sample T-test $p \leq 0.05$)
	Unable to perform T-test due to data supporting insufficient power
	Unable to perform T-test due to lack of data within one or more categories

Appendix V: comparable juvenile colony density values

Table 15. Juvenile colony density values (colonies per unit area) from this research compared with published data and comoparable unpublished studies

Publication Year	Author	Reef location	Habitat characteristics	Definition Juvenile (mm)	Juvenile colonies per m2*	Additional notes	
1979	Bak and Engel	Curacao and Bonaire	Drop-of zone (leeward reefs)	≤40	13-20	Low environmental stress	From Ruiz-Zarate, 2004
1983	Rylaarsdam	Jamaica	Fore-reef	<50	76-274	None	
1984	Rogers <i>et al.</i>	St. Croix, US Virgin Islands	Reef wall	≤40	13-33	depth gradient of 9-37m, average 18 colonies per m2	
1996	Chiappone & Sullivan	Florida reef tract	Relict supr and groove	<40	2-4	Degraded reef sites	
1997	Smith	Conch Reef, Florida	Low-relief spurs	<20	1-4	None	
1998	Edmunds <i>et al.</i>	Great Lameshur Bay, US Virgin Islands	<i>Montastrea annularis</i> knolls	≤4 to ≤50	4	None	
1999	Mumby	Glovers Atoll, Belize	Seaward fore-reef (nr atoll drop-off)	≤20	2-3	None	
2000	Miller <i>et al.</i>	Florida reef tract (Biscayne National Park)	Bank reefs	≤50	1	None	
2001	Edmunds & Carpenter	Jamaica	Fore-reef	≤20	2-42	11-42 <i>Diadema</i> zone, 2-12 algal zone	
2003	AGGRR database	Caribbean	Fore-reef	≤2 to ≤40	1-7	1-6.5 in 66% sites	
2004	Ruiz-Zarate & Arias-Gonzalez	Central and Southern Q.Roo State, Mexico	Fore-reef, spurs and grooves	≤20	1-6	From 8 reefs across 240km of Mesoamerican Barrier Reef System	
1991	Yeemin	Kuwashima, Japan	Rocky reef high latitude	≤40	4	None	
2007	Wilson	Chagos	Seaward reefs various depths	<50	70	Data collected 2001, sampled 'settleable' substrate only	
2007	Wilson	Southern Arabia	Coastal fringing reefs	<50	22	Data collected 2001, sampled 'settleable' substrate only	
1999	Obura 2002	Northern Kenya	Coastal fringing reefs	not specified	0	None	
2000	Obura 2002	Northern Kenya	Coastal fringing reefs	not specified	2	None	
2003	Obura 2002	Northern Kenya	Coastal fringing reefs	not specified	2	None	
2005	Souter and Linden	East African coast	Coastal fringing reefs	not specified	1	Considered 'substantial' density	
2000	McClanahan	Maldives	Seaward reefs	<50	29	Average, no statistically significant differences with depth	
2000	Edwards	Maldives, Male	Seaward reefs	<50	23	Data from 10 months post bleaching	
2006	Bianchi	Maldives	Seaward reefs	<50	5	Data from 2000, 2 years post McClanahan	
2000	Loch	Maldives	Seaward reefs, 10m depth	<50	4	Data from 21 months post bleaching	
2000	Loch	Maldives	Seaward reefs, dead <i>Acropora</i> tables	≤40	11	Data from 21 months post bleaching	
2008	Obura	Saudi Arabia, Al Wajh	Seaward reefs	≤50	26	Unpublished	
2008	Obura	Amirantes, Outer Seychelles	Seaward reefs	≤50	8	Unpublished	
2008	Obura	Northwest Madagascar, Nosy Hara	Fringing seaward reefs	≤50	4	Unpublished	
2006	Harris (this study)	Chagos	Seaward reefs	≤50	15	n=1307, from 809 replicate quadrats	
2008	Harris (this study)	Granitic Seychelles	Coastal fringing reefs	≤50	6	n=1208, from 1904 replicate quadrats	
2009	Harris (this study)	Saudi Arabia, Farasan Banks	Seaward reefs	≤50	48	n=1416, from 264 replicate quadrats	
2009	Harris (this study)	Saudi Arabia, Farasan Banks	Seaward reefs	<50	71	n=2069, from 264 replicate quadrats (with UV)	

* to nearest whole colony, including range where given*

Appendix VI: publication summary, May 2010

1 Publications during PhD

Ahamada, S., Bijoux, J., Cauvin, B., Hagan, A.B., **Harris**, A., Koonjul, M., Meunier, S., and Quod, J.-P. (2008) Status of the Coral Reefs of the South-West Indian Ocean Island State: Comoros, Madagascar, Mauritius, Reunion, Seychelles, in Wilkinson, C.R., ed., Status of the Coral Reefs of the World: 2008: p. 73–79

Gillibrand, C.J., **Harris**, A.R., and Mara, E. (2007) Inventory and Spatial Assemblage Study of Reef Fish in the Area of Andavadoaka, South-West Madagascar (Western Indian Ocean): Western Indian Ocean Journal of Marine Science v. 6, p, 183–197

Graham, N.A.J., Purkis, S.J., and **Harris**, A. (2009) Diurnal, land-based predation on shore crabs by moray eels in the Chagos Archipelago. Coral Reefs 28: 397

Harris, A., 2007, "To live with the Sea" Development of the Velondriake Community-Managed Protected Area Network, Southwest Madagascar: Madagascar Conservation & Development v. 2, p, 43–49

Harris, A., and Sheppard, C.R.C. (2008) Status and Recovery of the Coral Reefs of the Chagos Archipelago, British Indian Ocean Territory, in Obura, D.O., Tamelander, J., and Linden, O., ed., Ten years after bleaching - facing the consequences of climate change in the Indian Ocean. CORDIO Status Report 2008.: Mombasa, Coastal Oceans Research and Development in the Indian Ocean/Sida-SAREC, p. 61–70

Harris, A., Manahira, G., Sheppard, A., Gough C., Sheppard C. (2010) Demise of Madagascar's once great barrier reef - change in coral reef condition over 40 years. Atoll Research Bulletin v. 574 p, 1-18

Nadon, M.-O., Griffiths, D., Doherty, E., and **Harris**, A. (2007) The Status of Coral Reefs in the Remote Region of Andavadoaka, Southwest Madagascar: Western Indian Ocean Journal of Marine Science v. 6, p, 207–218

Sheppard, C.R.C., **Harris**, A., and Sheppard, A.L.S., (2008) Archipelago-wide coral recovery patterns since 1998 in the Chagos Archipelago, central Indian Ocean: Marine Ecology Progress Series v. 362, p, 109–117

Sheppard, C.R.C., Chen, A., **Harris**, A., Hillman, C., Graham, N.A.J., Marx, D., McGowan, A., Mortimer, J., Pfeiffer, M., Price, A.R.G., Purkis, S.J., Raines, P., Riegl, B., Schleyer, M., Sheppard, A., Smith, S., Tamelander, J., Topp, J.M.W., Turner, J., and Yang, S.Y. (2009) Science in Chagos: what we know and what we need to know. 24

Andriamalala, G. and **Harris**, A. (2008) Socioeconomic monitoring initiative for Velondriake community managed protected area, Madagascar. 405-408. In Obura, D.O., Tamelander, J. & Linden, O. (Eds). Ten years after bleaching – facing the consequences of climate change in the Indian Ocean. CORDIO Status Report. Coastal Oceans Research and Development in the Indian Ocean/Sida-SAREC. Mombasa.

Mangubhai, S., **Harris**, A., and Graham, N.A.J. (2006) Synchronous daytime spawning of the solitary coral *Fungia danai* (Fungiidae) in the Chagos Archipelago, central Indian Ocean: Coral Reefs v. Reef sites.

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2 In press:

Harris, A., Gibbs, R., Schleyer, J., Taylor, K., Sheppard, C. (2010) Safeguarding temperature loggers on remote coral reefs - lessons learned from relocating loggers in the Chagos archipelago. Reef Encounter

3 Under review:

Harris, A., Benbow, S., Gough, C. Recovery dynamics of coral reefs in Andavadoaka, southwest Madagascar: 2004-2008 (Biological Conservation)

Harris, A., The elephant in the lagoon - addressing the unutterable threat to marine sustainability (Oryx)

4 In preparation for submission with thesis:

Harris, A. and Sheppard, C.R.C. Coral communities of the Farasan Banks, Saudi Arabia

Harris, A. and Sheppard, C.R.C. Impact of Red Sea coral mortality on coral community composition and population structure

Harris, A. and Sheppard, C.R.C. Fluorescence surveying of juvenile corals improves accuracy of colony detection

Riegl, B., Purkis, S., **Harris, A.,** and Sheppard, C.R.C., Post-disturbance dynamics of coral populations in one of the world's least anthropogenically influenced reef systems (Chagos, Indian Ocean).

Humber, F., **Harris, A.,** Raberinary, D., and Nadon, M., Seasonal closures of no-take zones to promote a sustainable fishery for *Octopus cyanea* (Gray) in South West Madagascar

Oleson, K., **Harris, A.** and Humber, F. Cost-benefit analysis of an octopus no take zone in southwest Madagascar

5 Relevant awards and recognitions received during PhD

Warwick Biological Sciences Postgraduate Symposium presentation award (2010)

Winner, World Conservation Union Young Conservationist Award (2010)

Condé Naste Environmental Award (2009)

Runner up, World Conservation Union Young Conservationist Award (2008)