

# Scleractinian Coral Fauna of the Western Indian Ocean

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## ABSTRACT

Scleractinian coral species surveys were conducted at 10 sites in the western Indian Ocean, between 2002 and 2006. Each site varied from approximately 50-200 km in extent and was sampled with from 7 to 27 dives. Accumulation curves based on successive samples at each site were used to construct logarithmic regression curves, which provide estimated species numbers at each site at an arbitrary value of 30 samples per site, assumed to reflect the total number of species. The highest diversity of corals was found in southern Tanzania to northern Mozambique (from Mafia Island to Pemba town), with 280-320 species estimated per site. Species diversity was lower in the central Indian Ocean islands (140-240 species) and declined steadily to a minimum in northern Kenya (150 species). These patterns are consistent with the central coast (around 10°S in Tanzania/Mozambique) accumulating and retaining species due to the South Equatorial Current (SEC) and mixing/reversing currents locally, respectively. The islands may have restricted diversity due to low area but nevertheless be stepping stones to the East African mainland coast. Lower diversity northwards into Kenya may reflect distance and low dispersal from the center of diversity at 10°S, and poorer conditions due to the Somali Current influence in the north. Observer effects and unclear taxonomy of scleractinian corals may significantly affect the dataset, as may faunal changes

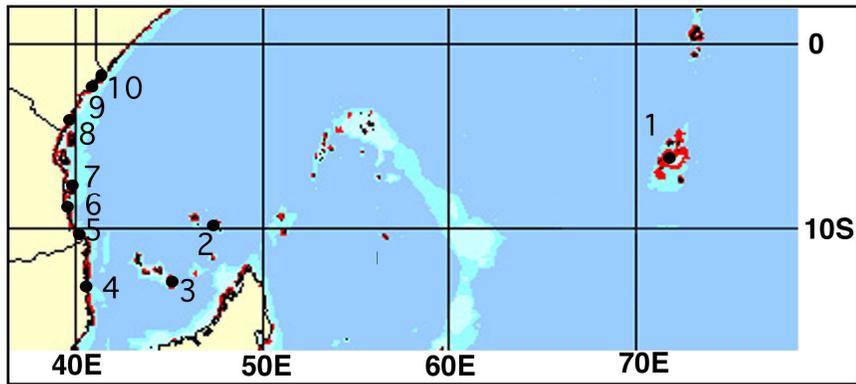
due to bleaching or other impacts at individual sites during the course of the study. Finally, it is likely that the diversity gradient northwards into Kenya is replicated southwards into southern Mozambique and South Africa, providing a means to test latitudinal changes in diversity and species distributions.

## INTRODUCTION

The scleractinian coral fauna of the western Indian Ocean (WIO) is one of the least studied globally. In global biogeographic assessments, it appears as a low diversity extension of the main West-Pacific center of diversity (Wells 1957, Rosen 1971, Veron 2000), now commonly called the 'Coral Triangle'. Typically, species numbers of 200-250 are quoted for the WIO, compared to 400-600 for Southeast Asia and Eastern Australia. The mainland East African coast often is depicted with higher species numbers than the islands of the central Indian Ocean, forming a regional center of diversity.

In regional analyses, the East African mainland coast and parts of Madagascar show higher levels of species diversity, with the islands and peripheral seas (Red Sea, Arabian Sea and Gulf of Aden) showing lower diversity. Due to transport of coral larvae westwards in the South Equatorial Current, there is a shorter systematic difference between sites east-west across the Indian Ocean, compared to north-south (Sheppard 1987). Along the African coastline, the

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**Figure 1.** Map of the Western Indian Ocean showing the study sites numbered from 1 to 10 (see Table 1). Map source: Reefbase.

SEC splits at about 10°S, with one arm flowing northwards as the East African Coastal Current and the other southwards in the Mozambique Current.

This study updates the coral species diversity of a part of the WIO taking advantage of improved resources for field-based identification of species (Veron 2000, Wallace 2000, Sheppard and Obura 2005). The region examined extends in a transect from east to west in the SEC from 72 - 40°E ( $\approx 3500$  km) and from south to north in the flow of the EACC from 12 - 2°S ( $\approx 1500$  km).

## METHODS

Sites were defined by the scope of survey expeditions, but were generally consistent as being reef systems of some 50-100 km extent in a consistent geomorphological unit. The largest site surveyed was the Chagos archipelago, and the smallest was individual reefs around Mombasa, Kenya, and Pemba, Mozambique.

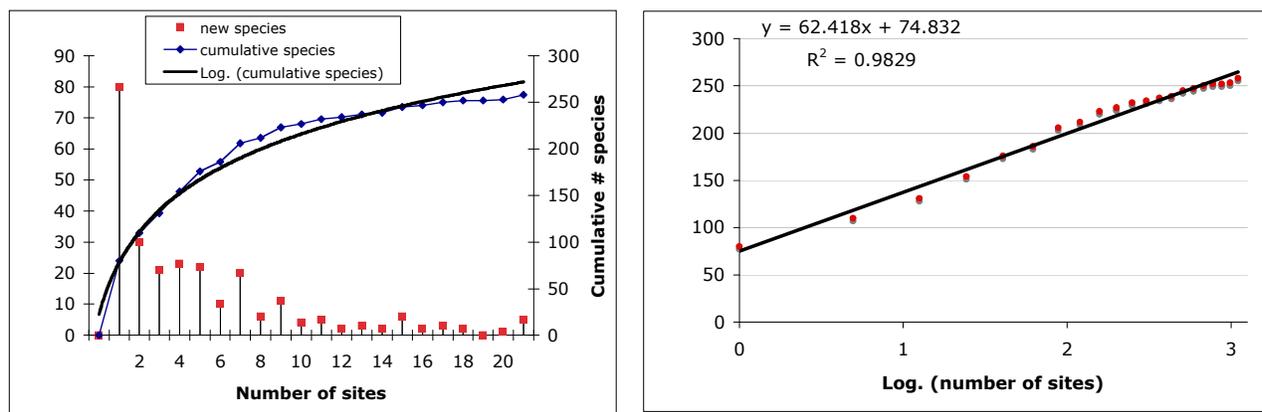
Species inventories during individual dives were made, generally lasting 30-60 minutes and extending over the full range of depths at a site from deep to shallow. In an excel spreadsheet, the number of previously unseen species in successive samples were counted, and combined together to form an accumulation or rarefaction curve for the location (Salm 1984). Identification of species was done in situ assisted by digital UW photography, collecting a full

inventory focusing on unusual or difficult species for photographs (Sheppard and Obura 2005). In cases of uncertainty collected skeletons were further examined after the dives. The principal resources used in identification were Veron 2000, 2002 and Wallace 2000.

In this study, a 'species' is defined operationally as a form that is distinguishable according to visual observation of the live colony against criteria presented in relevant texts (Veron 2000, Wallace 2000). The problems of morphological variation and plasticity, hybridization and biological species boundaries cannot be dealt with beyond this level. Thus the 'species' here is a hypothesis that is primarily based on its utility in field observation, and may change with new information and taxonomic work.

## Curve Fitting

One of the simplest curves fitting the accumulation of species with successive samples is a logarithmic curve (Fig. 2). These closely fit existing data points, often with  $r^2$  of over 0.9 and even 0.95. A further advantage is that on a semi-logarithmic scale they transform into a straight line, and the two coefficients of the curve can be easily interpreted: the intercept with the y axis is indicative of the diversity at an individual site level (within-site species-packing, i.e. alpha diversity), while the slope is indicative of diversity of species between sites (i.e. between-site variability or heterogeneity in the species pool, i.e. beta diversity). A logarithmic



**Figure 2.** Illustration of number of new species, cumulative curve and logarithm regression of the cumulative species data points (left). Transformation of the logarithmic curve to a straight line (right) with the regression equation and  $R^2$  value.

**Table 1.** Site and sampling details, western Indian Ocean, 2002-6.

Locations			Sampling			Coordinates			
Area (#)	Country	Year	Days	samples	hours	Lat S	min	Long E	min
Chagos – 1	UK	2006	22	27	15.2	6	30.0	72	0.0
Cosmoledo–2	Seychelles	2002	9	7	7.5	9	45.1	47	37.2
Mayotte – 3	France	2005	14	18	10.2	12	52.8	45	16.6
Pemba – 4	Mozambique	2003	3	7	5.3	12	58.3	40	32.4
Mnazi Bay – 5	Tanzania	2003	10	7	10.1	10	18.9	40	23.3
Songo Songo-6	Tanzania	2003	5	7	13.4	8	30.0	39	55.0
Mafia – 7	Tanzania	2004	8	16	13.5	7	56.9	39	47.3
Mombasa – 8	Kenya	2005	10	13	9.0	4	3.7	39	42.7
Lamu – 9	Kenya	2005	4	8	5.1	1	57.8	41	18.3
Kiunga - 10	Kenya	2005	7	15	11.7	2	18.9	41	0.4

curve however, has one major drawback for fitting species accumulation curves, as the maximum number of species in a region is limited, whereas the logarithmic curve does not asymptote – with infinite samples the curve predicts an infinite number of species. Operationally however, a maximum level of sampling can be defined for the pool of locations within a study. For the purposes of this study, a maximum sampling level of 30 sites was selected, slightly higher than the maximum sampling levels that were undertaken at Kiunga (23) and Chagos (27).

## RESULTS

The dataset includes 10 locations in the central and western Indian Ocean (Table 1), from the Chagos Archipelago in the east, through the Seychelles and Comoro Islands to the central section of the East African mainland coast in northern Mozambique and southern Tanzania, and northwards to the northern Kenya coast. Surveys were conducted from 2002 to 2006, and varied from a minimum of 3 days and 7 samples to 22 days 27 samples.

**Table 2.** Coral species diversity for sample locations. Measured number of species, predicted number of species for 30 samples, and regression results.

Site	Number of species		Regression statistics		
	Measured	Predicted	Exponent	Intercept	r <sup>2</sup>
Chagos	240	248	57.15	53.57	0.980
Mayotte	222	237	43.62	88.74	0.972
Cosmoledo	143	170	34.27	52.95	0.835
Pemba	206	297	61.40	88.22	0.974
Mnazi	258	288	62.39	75.41	0.984
Songo	206	244	59.16	42.76	0.955
Mafia	268	320	67.11	92.22	0.969
Mombasa	241	262	46.92	102.14	0.841
Lamu	157	245	59.31	43.26	0.952
Kiunga	154	188	48.99	21.15	0.973

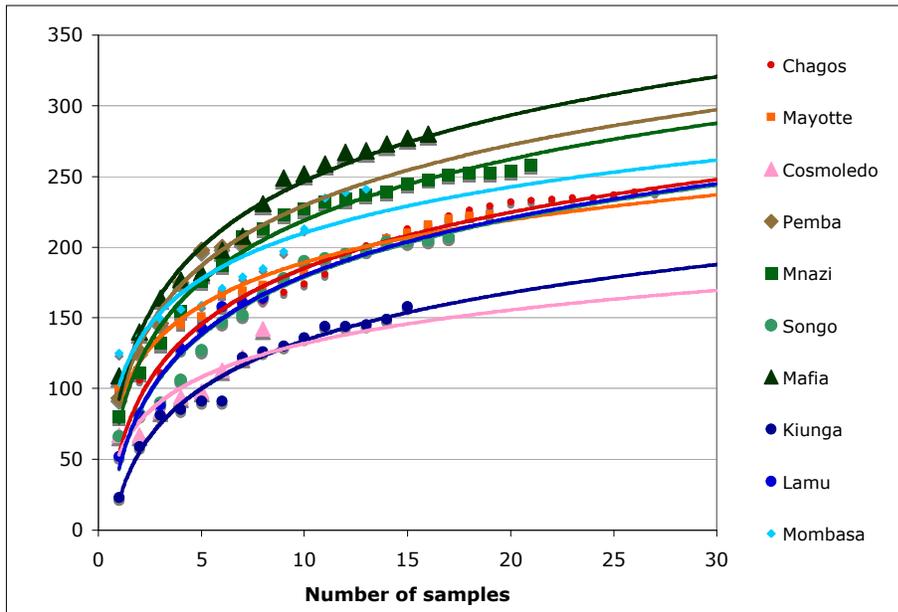
Actual species numbers varied between 143 and 268 (Table 2) per site, and was correlated with the degree of sampling (# days,  $r = 0.396$ , # samples,  $r = 0.359$ ), however with a high degree of variation. Logarithmic regression curves on the cumulative number of species in successive samples at each site (Fig. 3) give highly significant  $r^2$  values of 0.841-0.984 (Table 2). At a hypothetical sample size of 30 per site, predicted species number was highest for Mafia (320), Pemba (297) and Mnazi (288), and lowest for Kiunga (154) and Lamu (157, Table 2), from 7 – 44% greater than measured species number (Fig. 4). The discrepancy between measured and predicted species number was greatest for Lamu (56%) and Pemba (44%), which were among the least-sampled sites (8 and 7 samples, respectively), and least for Mayotte (7%) and Chagos (3%), the last sites to be sampled (2005 and 2006 respectively) and with the highest degree of sampling (18 and 27 respectively).

A cluster analysis (Fig. 5) of coral species presence/absence clearly grouped the southern Tanzania/northern Mozambique sites together, and the larger

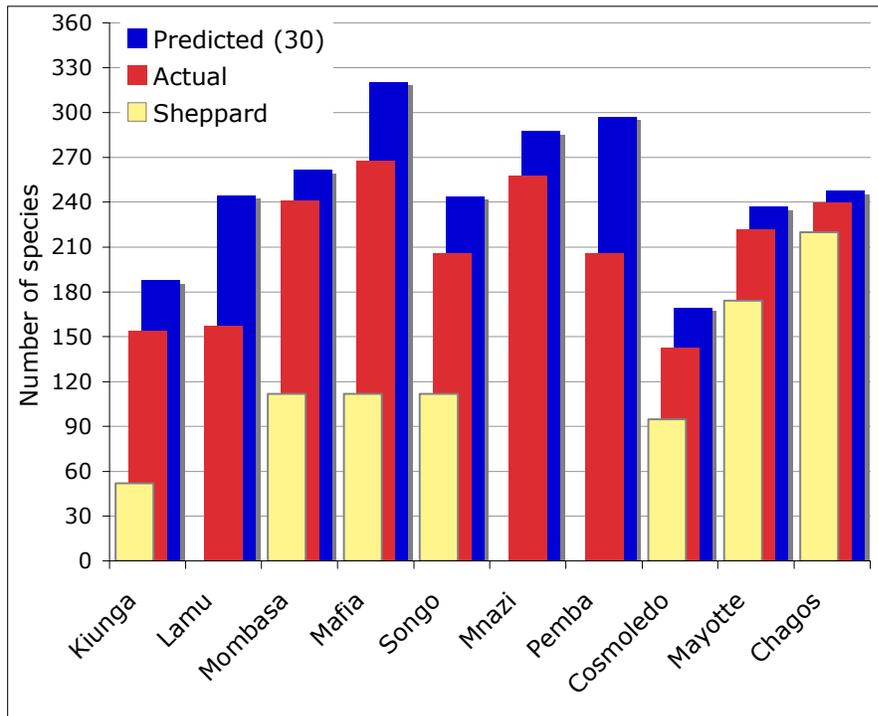
island sites (Chagos and Mayotte) to these. Sites in Kenya formed an outgroup, with Lamu and Kiunga most similar to each other. The grouping clearly matches the geographic spread of the sites, the only discrepancy being the tendency of Cosmoledo (2 on the map) to group with the mainland sites before the other island sites. This may be an artifact of sampling as Cosmoledo was the earliest of the samples included in this analysis and one of the least-sampled sites, raising the probability of errors in the dataset due to inexperience and sampling artifacts.

## DISCUSSION

Biogeographically, surveys cover a consistent region defined by the South Equatorial Current (SEC) as it sweeps from east to west across the island systems in the equatorial Indian Ocean, and the north-flowing East African Coastal Current (EACC) that starts where the SEC hits the African mainland coast. The southern-most sample, at Pemba, Mozambique is likely in the southern flow of the Mozambique



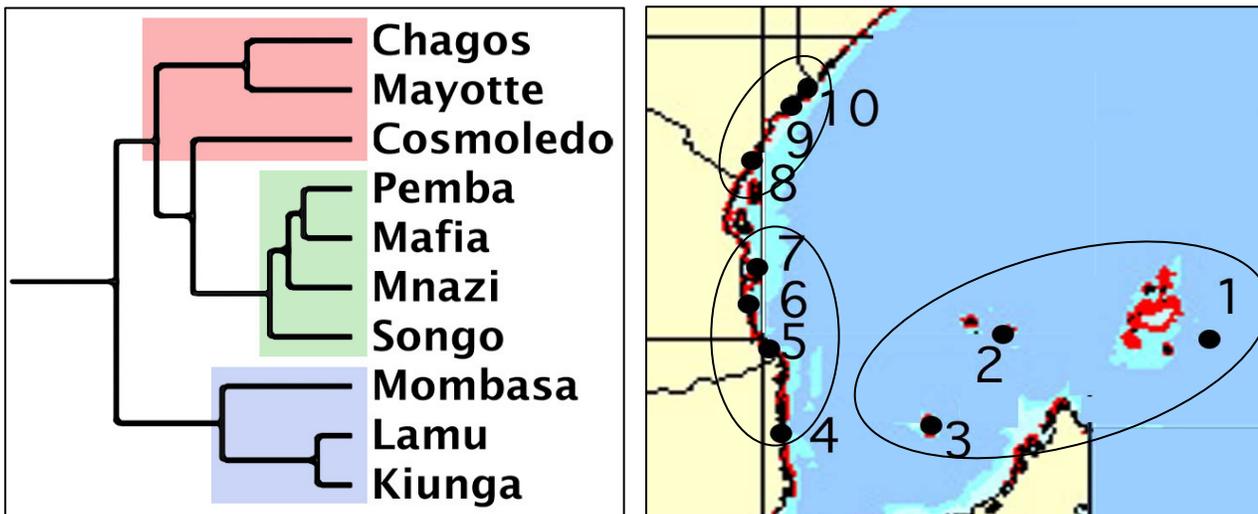
**Figure 3.** Accumulation curves for all sites coded by colour – red (islands), green (Tanzania-Mozambique), blue (Kenya).



**Figure 4.** Number of species for each of the sample locations. The predicted and actual numbers are shown, along with values from the literature reported in Sheppard (2002).

**Table 3.** Factors contributing to the observed diversity patterns for the scleractinian coral fauna of the western Indian Ocean.

Region	Southern Tanzania/ northern Mozambique	Kenya (likely includ- ing northern Tanzania)	Central Islands
Diversity	High	Low	Low
Factors	<p>inflow of the SEC carrying larvae from the Indonesian region.</p> <p>mixing over the large area of continental coast that may cause retention of larvae.</p> <p>large area of continental coastline (compared to smaller areas of the central islands) may result in a species-area effect.</p>	<p>uni-directional flow of the EACC results in declining species number with distance from the center of diversity.</p> <p>marginal conditions caused by upwelling in the Somali Current system may reduce species diversity due to poorer conditions for survival of larvae and/or adults.</p>	<p>uni-directional flow of the SEC preventing accumulation and retention of species.</p> <p>area effect of small islands resulting in lower species number.</p> <p>steep-sided oceanic island and platform systems may provide limited area for coral growth.</p>

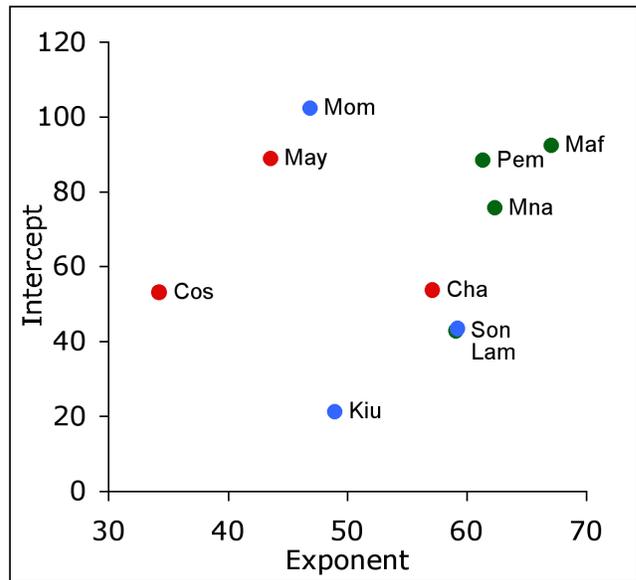


**Figure 5.** Cluster analysis and regionalization of study sites according by presence/absence of species.

current, though recent evidence shows this southerly flow to be highly variable, alternating between periods of apparent low net flow, and large eddies that move southwards down the Mozambique Channel (Lutjeharms 2007). The northern Mozambique-southern Tanzanian region may thus experience a high level of variable currents and mixing, and form a single region. From this region, the EACC flows consistently northwards, meeting the reversing currents of the Somali Current (SC) system before the northern-most sites in Lamu and Kiunga, Kenya (Johnson et al. 1982). This gradient northwards into Kenya is replicated southwards into southern Mozambique and South Africa, though currents may not be as linear as occurs in the EACC, and cooler water conditions as a result of the Agulhas Current in the south may have a different effect from the upwelling Somali Current in the north.

The regionalization provided by the cluster analysis (Fig. 5) and predicted species richness of the sites (Table 2, Fig. 3) support the notion that southern Tanzanian/northern Mozambique is a single region, and that it is a center of diversity for the western Indian Ocean. Lower diversity is found in the islands upstream in the SEC – thus while these do act as stepping stones that feed propagules into the region from the Indonesian region, there is a larger species pool of western species (mainland Africa and Madagascar) not found in the islands. Diversity also declines northwards along the linear coastline from Tanzania to Somalia (Table 3), likely a result of distance-dispersal factors, declining complexity of the coastline resulting in lower reef area and structural diversity, and less suitable conditions for coral survival in the higher-nutrient lower-temperature waters of the Somali Current system.

This analysis predicts 320 species for the Mafia Island coral reefs, and numbers near this level for adjacent sites. Taking into account beta-diversity between the sites reported here, and of more cryptic and non-reefal scleractinians that were likely excluded from this study, it is likely that the total species count for WIO scleractinians would top 350, and probably even 400 species. This is within the range of the



**Figure 6.** Scatterplot of regression coefficients (exponent vs. intercept).

species diversity reported for the Great Barrier Reef, a region of equivalent size, and even to the outer edges of the Coral Triangle around eastern Papua New Guinea and the Solomon Islands (Veron 2000). This increase in species number over historical records of < 200 (Hamilton 1975, Hamilton and Brakel 1984, Sheppard 2002) is also due to increasing taxonomic focus in the WIO and surrounding seas. Recent works (Riegl 1995a,b, Veron 2002 and Turak et al. 2007) illustrate the potential for new species descriptions from the region, further supported by a number of uncertain species (Mangubhai 2007, pers. obs.). With increased taxonomic work in the region, significant revisions of the accepted notion of Indo-Pacific coral biodiversity will be required.

The coefficients of the regression curves define ‘assembly rules’ for each site’s fauna – the y-intercept relates to the number of species at a single site (alpha diversity) and the exponent to the heterogeneity of species among site (beta diversity), i.e. the rate of new species encountered from one site to the next. Plotting exponent and intercept for the sites (Fig. 6) shows that the high-diversity sites of southern Tanzania/northern Mozambique principally had both high exponents and

intercepts. The island and Kenya sites were intermingled, with the island sites tending to have low exponents (Cosmoledo and Mayotte), signifying homogeneous species complement across sites, and the northernmost Kenya sites have low intercepts, signifying a low number of species at each site. Relating these to biogeographic processes, this suggests that high diversity in southern Tanzania/northern Mozambique is due to high alpha and beta diversity (high species packing within sites, large species pool with high mixing among sites), island sites have low beta diversity (consistent species pool with high mixing/low differential between sites) and northern Kenya sites have low alpha diversity (small species pool).

Visual identification of coral species underwater has always been problematic as primary taxonomic descriptions are based on preserved skeleton samples with no reference to live tissue characteristics. However increasingly *in situ* identification is being done and accepted in the literature (Sheppard and Obura 2005). However, there are specific issues that affect this type of dataset:

- A significant change in resources in the period 2000-3, marked by the publication of Veron (2000, 2002) and Wallace (2001) and related outputs such as the accompanying CDs. While this has improved this dataset, the learning curve from the first (2002) to last (2006) surveys is significant.
- The advent of digital photography over the same time period allowed immediate investigation of photographic records after a dive for verification with references and other observers.
- Observer experience is critically important, and with regular surveys increases over time. As found here, early samples tend to contain fewer species than later ones, particularly found for Cosmoledo and Pemba samples, and exacerbated by their small sample sizes.
- The high morphological plasticity of corals has always made identification difficult, and this is magnified when a colony is not collected or

retained for verification afterwards. This is particularly important where intermediates and potential hybrids among closely related species vary in abundance, as often a decision on whether they are scored as a species depends on having visual references to the whole series at hand. Thus where species diversity is high and corals are abundant it is possible that more species will be more consistently scored, than where diversity and abundance are lower, and divergent forms are more likely to be lumped together for lack of visual references.

A final word of caution on this type of dataset is that samples are spread over a broad range of years, here from 2002-6. In a time of rapid change and increasing water temperatures major disturbance events such as bleaching may occur at some locations but not others, and between sampling periods (e.g. see for Egmont in Chagos, in Harris and Sheppard, 2007). Thus differences in diversity may reflect factors other than the biogeography and distribution of species.

The logarithmic curves used here have very high significance with  $r^2$  values approaching 0.99. As predictors of species number at an arbitrary number of samples (e.g. 30), they therefore perform well. However theoretically they do not reflect the fact that the total number of species in a site must have a maximum (at or below the total number of coral species in the region), while logarithmic curves do not asymptote. Further work is needed to develop a regression curve that fits the data points as well as a logarithmic function, but has an asymptote to enable a theoretical (not arbitrary) maximum number of species for a site or region.

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