

The influence of habitat structural complexity on invertebrate diversity: A comparison between an impacted and a pristine coral reef

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The influence of habitat structural complexity on invertebrate diversity: A comparison between an impacted and a pristine coral reef

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Abstract

Habitat complexity is shown to be an important driver of invertebrate diversity on impacted coral reefs when the diversity supported by a comparative unit of habitat complexity is compared to that of a pristine coral reef. The more structurally complex pristine reef does not support the conventionally expected greatest amount of diversity, instead an upper limit threshold to habitat complexity is observed. These findings demonstrate the importance of structural complexity on coral reefs to the associated invertebrate communities and marks habitat complexity as a factor to consider in coral reef conservation planning.

Introduction

The increase in the diversity and/or abundance in fauna related to the increase in habitat complexity is generally acknowledged (Crooks, 2002; Bourna *et al.*, 2009; Cruz Sueiro *et al.*, 2011). The fundamental hypothesis to this is that more structure provides more resources, habitats and niches (Connor & McCoy, 2001; Cruz Suerio *et al.*, 2011). Various authors (MacArthur & MacArthur, 1961; Lawton, 1983; Ellner *et al.*, 2001; Kelaher, 2003) have shown that the physical characteristics of habitats also affect the associated community structure. More heterogeneous and complex environments have greater diversity of organisms as stated in the spatial heterogeneity hypothesis (Valiela, 1995; Kelaher, 2003). This pattern is generally ascribed to the concept that increased availability of resources occurs as more surface area, which accompanies greater structural complexity, becomes available (Connor & McCoy, 1979; Kelaher, 2003). From this concept it follows that an increase in available area or structural heterogeneity will be accompanied by an increase in the number of possible micro-habitats or niches (MacArthur & MacArthur, 1961; Schoener, 1974; Kelaher, 2003). This is confirmed by Begon, Harper & Townsend (1996) who state that more spatially heterogeneous environments can be expected to contain more species because of the provision of a greater variety of microhabitats as well as more hiding places from predators.

Would spatial heterogeneity still be an important factor for diversity if habitat disturbance occurred? According to Bonin, Almany & Jones (2011) disruption of the habitat can

result in fragmentation or loss of appropriate habitat and in some cases both, which in turn influences the survival of species, their interactions and subsequent patterns of diversity in the area. Numerous studies have been done which advocate that the effects of habitat loss on biodiversity are persistently negative, in contrast the studied effects of fragmentation are every so often, counter intuitively, positive (Bonin, Almany & Jones, 2011).

Coral reefs are prime examples of structurally heterogeneous habitats; unfortunately these habitats have been greatly impacted globally by: overfishing, coral bleaching due to climate change, eutrophication and disease (Alvarez-Filip *et al.*, 2009). The complexity of coral reefs has been shown to positively influence biodiversity by facilitating species cohabitation through niche partitioning and refuge provision to escape predation and environmental stressors (Knudby & LeDrew, 2007; Alvarez-Filip *et al.*, 2009 and references therein). This leads us to expect biodiversity to increase with an increase in coral reef structural complexity. It has been proposed that a loss of structural complexity in coral reefs may drive declines in diversity especially in specialist species (Beukers & Jones, 1997; Graham *et al.*, 2007 in: Alvarez-Filip *et al.*, 2009). Factors that contribute to loss of complexity are both natural (hurricanes, high densities of coralivores, coral disease outbreaks, etc.) and anthropogenic. This creates the expectation that impacted reefs would be less diverse than pristine reefs. Although many ecologists are of the opinion that disturbance may be the most powerful way in which diversity can be generated (Begon, Harper & Townsend, 1996). Pandolfi & Jackson (2007) summarize and explain this opinion as follows: disturbance events occur at a variety of temporal and spatial scales and the abundance of species are in a continuous state of recovery from these disturbances, although the time that elapses between these events as well as the intensity of the disturbances can have strong effects on the community structures and compositions. The intermediate disturbance hypothesis discussed by Wilson (1994) also addresses this phenomenon of increased diversity in habitats exposed to disturbance events. The intermediate disturbance hypothesis states that disturbance events serve to clear areas in the habitat which are then open for colonization. This adds to the diversity within the habitat if the disturbance is not too frequent or too rare.

It is crucial, in view of the present global degradation of coral reefs, that the relative role of different processes (Pandolfi & Jackson, 2007) and factors in the preservation of reef

diversity be determined.

Some of the most diverse coral reefs in the world are located in Indonesia with Eastern Indonesia being the center of the Coral Triangle, the global coral biodiversity hot spot (Edinger *et al.*, 1998). Apart from sustaining great biodiversity, the structural complexity of coral reefs contributes to coastal protection through dissipation of wave energy transmitted over reefs (Lugo-Fernandez *et al.*, 1998 in: Alvarez-Filip *et al.*, 2009). In coastal settlements this form of protection is invaluable. According to Edinger, Kolasa & Risk (2000) Indonesia's coral reefs are threatened by land-based pollution, overexploitation, destructive fishing methods (e.g. bomb fishing), oil spills and numerous forms of anthropogenic damage.

The relation between structural complexity (in all marine habitats, i.e. coral reefs, sea grass meadows, kelp forests, rocky reefs etc.) and fish biodiversity has received a significant amount of attention in literature and most of these studies have drawn the conclusion that high structural complexity is positively correlated with overall fish species diversity (Knudby & Le Drew, 2007). Similar studies for invertebrate diversity are mainly focused on intertidal zones or sea grass meadows, with very little done on the relation between structural complexity of coral reef habitats and invertebrate diversity. Grabowski & Powers (2004) summarized the findings of most of the studies done on invertebrate diversity and habitat complexity as follows: macro-invertebrate diversity and density are most commonly positively correlated with structural complexity. Is this also true for invertebrate diversity on coral reefs? For this reason this study will focus on invertebrate diversity on coral reefs. Published literature lacks comparative studies on the importance of habitat structural complexity for invertebrate diversity on impacted versus pristine coral reefs which leaves the unanswered question: is habitat structural complexity a more important driver for invertebrate diversity on impacted reefs than on pristine reefs? I hypothesize that the invertebrate diversity relative to habitat structural complexity will be greater on an impacted reef than on a pristine reef. This might seem counter intuitive, but when we consider that the impacted reef has fragments of intact coral reef habitat which might serve as a type of oasis in the midst of the coral rubble "desert" with regards to available resources and structural complexity, then relative to habitat structural complexity these hubs could contain more invertebrate diversity. This is sometimes referred to as the positive effects of fragmentation and may result from: an increase in immigration (to the patch of intact coral) (Greig *et al.*, 2004),

decreased competition for resources (Collins & Barrett, 1997; Wolff, Schaubert & Edge 1997; Caley, Buckley & Jones, 2001), or reduced abundance of predators (Hovel & Lipcius, 2001) in the fragmented habitat (Bonin, Almany & Jones, 2011).

To test this hypothesis the species diversity supported per unit habitat complexity (diversity-to-complexity ratio) on an impacted reef needs to be compared to that of a pristine reef. To accomplish this a value for habitat structural complexity is needed as habitat structural complexity consists of many different yet connected factors. When addressing the multivariate problem of habitat structural complexity, different aspects of habitat structure and composition need to be considered (Gratwicke & Speight, 2005). These aspects according to Gratwicke & Speight (2005) include: topographic complexity (rugosity), substratum diversity, variety of refuge hole size, vertical relief or height of substratum architecture, percentage live cover (effectively describes the cover of sessile fauna), and percentage hard substratum; which are all summarized by a habitat assessment score (HAS). Furthermore the diversity supported by the structural complexity should also be numerically expressed which is possible by using any of the numerous diversity index values. Species diversity takes into account the species richness and relative abundance of species within a community (Begon, Harper & Townsend, 1996). Indices that express the species richness element of diversity and indices that reflect the degree of dominance in the data should be calculated to give a complete representation of the diversity (Magurran, 2004).

The aims of this study are: 1) to establish the range of habitat complexity, using the HAS system, on an impacted and a pristine coral reef; 2) to establish if depth influences habitat structural complexity; 3) establish habitat complexity (HAS) categories which will be used in demarcating areas to 4) identify and quantify invertebrates; and finally 5) determine invertebrate species diversity and similarity on the two reefs.

Materials & Methods

Study site: The two reef habitats that served as the impacted and pristine reef sites are Sampela and Hoga respectively. These reefs are located in the Wakatobi Marine National Park which is located in the Tukang Besi archipelago, a secluded island group of about 200,000 ha off South East Sulawesi in Indonesia. The less impacted or pristine reef is found at Hoga Island, on which the Operation Wallacea Marine Research station is based, and has been protected from bomb fishing and coral mining practices. The

impacted reef is located near the Bajo village of Sampela, approximately 1.5km away from the Hoga home reef, and the practice of bomb fishing has severely damaged this reef with most parts of the reef being reduced to coral rubble; this has also led to more turbid water and thus less light availability. Each reef had essentially two dive sites: Sampela 1 and 2 on the impacted reef, and Buoy 3-4 and Pak Kasim's on the pristine reef, Figure 1

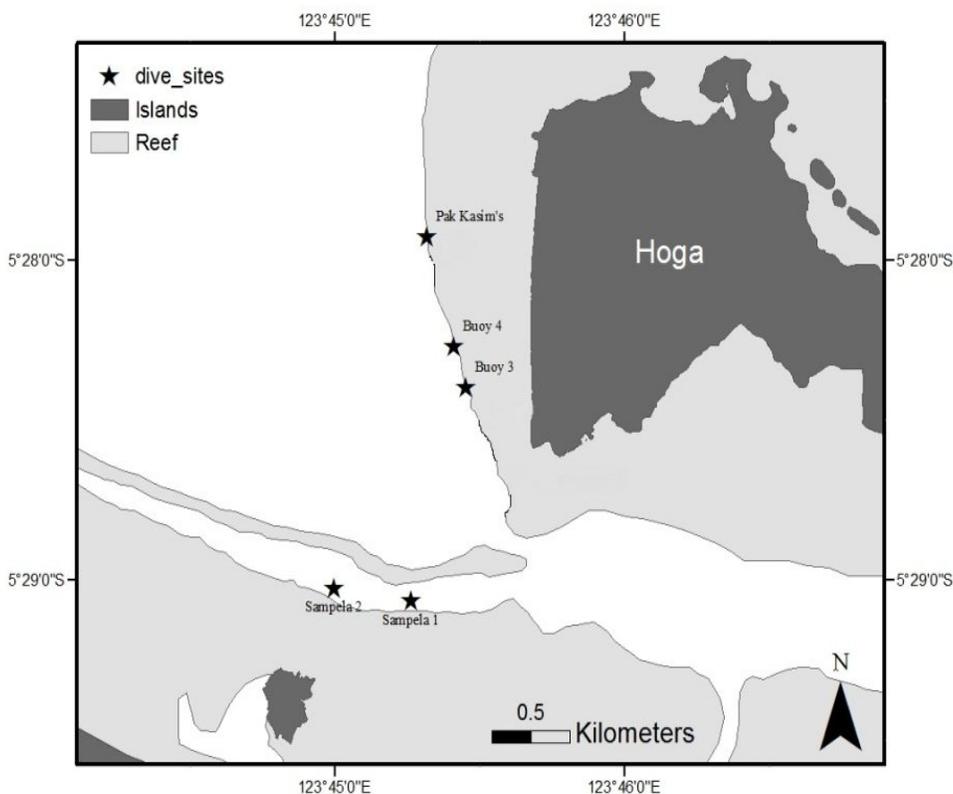


Figure 1. Locations of the dive sites where data was collected are indicated by stars.

Data collection: Data was collected through SCUBA diving, and a standard dive profile of maximum dive depth 18m and maximum dive time 50min surface to surface, including a 5min safety stop at 5m, was followed. Throughout the study a 1m² negatively buoyant quadrant (divided into 25 squares, each representing 4% of the total quadrant) was used to demarcate the area to be assessed following Gratwicke & Speight (2005) Habitat Assessment Score (HAS) system, Figure 2. This HAS sheet (Gratwicke & Speight, 2005) was laminated and attached to a dive slate for reference during each dive. Each quadrant was visually assessed for each aspect of HAS and the total scores recorded on a slate.

Data collection was divided into two phases. In the first phase HAS values were recorded across a depth gradient, including the following areas on the reef: reef crest (approximately 5m on Hoga and 2m on Sampela), mid depth (5m below reef crest) and

deep (10m below reef crest); to establish if depth influences habitat structural complexity.

	HAS SCORE				
	1	2	3	4	5
Rugosity (visual topographic estimate of the substratum in each quadrat)					
Variety of growth forms (stalked/lobed/filamentous/ribbon-like/massive/branching/cylindrical/tube/fan/plate/pinnate/encrusting/other)	<2	3 & 4	5 & 6	7 & 8	9-10
Height (visual estimate of average height of habitat architecture) (cm)	0-9	10-19	20-39	40-79	>80
Refuge size categories (holes or gaps in habitat architecture or substratum in the following size categories: 1-5, 6-15, 16-30, 31-50 and >50cm)	0-1	2	3	4	5
Live cover (total per cent cover of e.g. living corals, mangrove roots, seagrass, macroalgae and sponges)	0-19	20-39	40-59	60-79	80-100
Hard substratum (%)	0-19	20-39	40-59	60-79	80-100

Figure 2. The HAS score sheet following Gratwicke & Speight (2005).

The range of HAS on each of the reefs was determined in order to establish habitat complexity categories. In order to categorize the HAS values a means to standardize these values that would be categorized into these categories was necessary. Standardization was accomplished by treating each HAS value in its respective range as an ordinal unit. For example: if the HAS values ranged from 12 to 19 this range would contain 8 units. The HAS value of 12 would be the 1st unit, 13 would be the 2nd unit and so on. Then these ordinal units were converted to percentages this was accomplished by dividing the ordinal unit number by the total number of units in the specific range followed by multiplication with 100 for the percentage. For our example then 12 would represent 12.5%, 13 would represent 25% and so on. Using the HAS range values obtained from randomly assessing samples on each reef, three HAS categories (low, medium (med) and high) could be generated. These categories make it possible to compare the two reefs even though their range of habitat complexity is different. The HAS categories are defined by percentage brackets. The low category ranges from 0 – 20%, the med category from 40 – 60%, and the high category from 80 – 100%. Based on these percentages the HAS values from the respective ranges where

categorized with the low category including HAS values within the 0-20% interval, the med category included those HAS values with percentages between 40-60%, and the high category included HAS values with percentages ranging from 80-100%. The 20% gap between these categories was established in an effort to have clearly distinct complexity levels that could be compared.

A regression analysis was done to determine if there is any relation between depths (independent variable) and structural complexity of the reefs i.e. HAS values (dependent variable). This was done in Microsoft Excel by plotting the data as a scatterplot and fitting a “trend line” which provided the equation of the line of best fit along with the R^2 value. The results from these regressions would influence the phase two data collection.

The second phase of data collection encompasses actively seeking out areas within a specific HAS category and then identifying and quantifying the invertebrates within these sites. Sites that had HAS values in each category (low, med and high) were actively searched for on each reef regardless of depth (see Results of the HAS-depth regression). The invertebrates within the quadrant were identified and counted – 20minutes was spent on each quadrant – this data was recorded on a dive slate. Organisms were identified in field as much as possible to family level and with later analysis of photographs it was possible to identify the organisms to genus level and to ensure that identification was as accurate as possible infield notes were made of characteristics. Photos were taken with a GoPro, Hero HD2 with flat faced underwater casing. To positively identify organisms various references, provided by the Marine Research Station, were used (Aw, 1997; Allen & Steene, 1998; Debelius, 2004). Even though most organisms were positively identified to genus level there were some organisms that could not be identified to this level and thus for the calculations only the data up to family level is used. For the purpose of calculating the various indices, invertebrates that were counted exclude soft corals and corals.

Diversity and Similarity measures: Various diversity indices were calculated following the formulae shown in Magurran (2004). The following indices:(Family) Richness, Shannon’s (Shannon 1948), Simpson’s (Simpson 1949) and the reciprocal, Margalef’s (Clifford & Stephenson 1975), Menhinick’s (Whittaker 1977), log series or alpha (Fisher *et al.* 1943) and McIntosh U (McIntosh 1967); were calculated for invertebrate families recorded from each of the five samples in each HAS category for each reef. Using PAST software multivariate analyses of variance (MANOVA) was performed to establish

if there was any significant difference between the invertebrate diversity on the two reefs and between the three HAS categories. The abundance of the various families for each sample in each HAS category was used to calculate Bray-Curtis similarities (Bray & Curtis 1957) which were used as distances in non-metric multidimensional scaling (NMMDS) and cluster analyses to group the data which are most similar. NMMDS (an ordination technique) was done in PAST using the Bray-Curtis similarity measure. A Shepard's plot was done, using PAST, to determine the goodness of fit of the NMMDS solution. In the Shepard plot, a narrow scatter around a 1:1 line indicates a good fit of the distances to the dissimilarities. A stress value is also calculated for the Shepard's plot and is another measure of goodness of fit, these stress values range from 0 – 1, with large values indicating poor fit. If the fit is poor, then visualization could be misleading (Jongman *et al.*, 1995). Cluster analyses were also used to more clearly show how the different HAS categories from each reef were related with regards to Bray-Curtis similarity measures.

Ratio of diversity supported per complexity unit: To compare the diversity supported by the respective reefs per unit of complexity a ratio is calculated using: the averaged value of all the diversity indices calculated for the specific HAS categories on the respective reefs; and the average HAS values of the values within the range used to establish the HAS categories on the respective reefs. The ratio is further simplified by dividing the average diversity with the average HAS value which gives us a number which expresses the average diversity supported per unit habitat complexity. A Sign test is performed in PAST to compare these average diversity per unit habitat complexity values in each HAS category and each reef.

Results

The HAS ranges were 12-27 and 17-28 for Sampela reef and Hoga reef respectively. HAS values in the various categories are as follow: Sampela: low [12;14], med [18;20], high [24;27]. Hoga: low [17;18], med [21;23], high [26;28]. With regards to the regression between HAS score and depth only weak relations were found at the study sites (Figure 3 – 4). All the families identified on the respective reefs and their counts are summarized in the table below, Table 1. The diversity indices calculated from the collected data is summarised in Table 2.

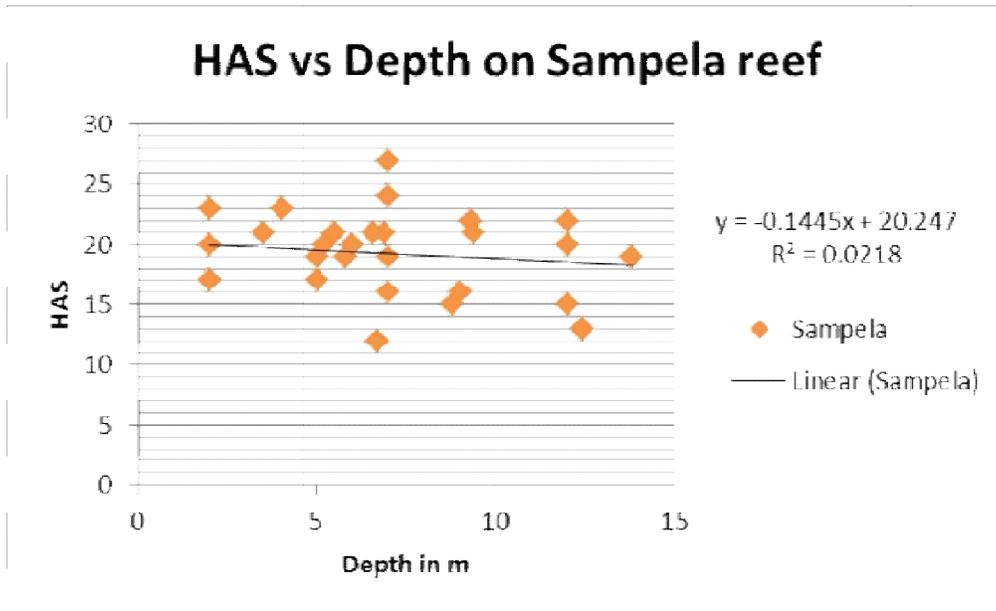


Figure 3. There is a very weak relation between the HAS score and depth at Sampela with the R^2 value indicating that 97.82% of the variation in HAS score is not accounted for by variation in depth.

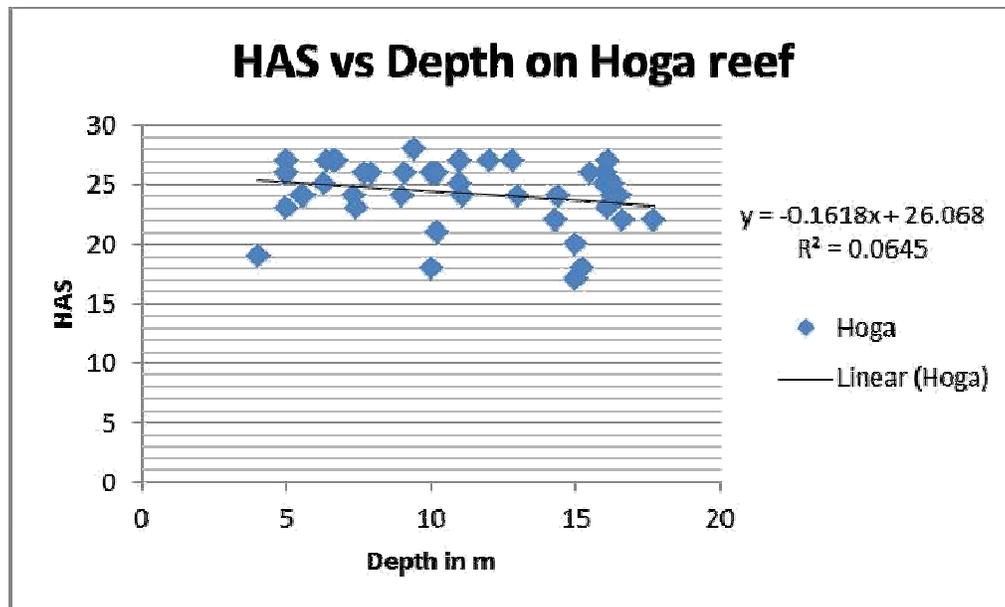


Figure 4. HAS and depth are weakly related. The R^2 value indicates that 93.55% of the variation in HAS values is not accounted for by variation in depth.

Table 1. The identified families and the total number of individuals in each family from the respective reefs.

Family	Hoga	Sampela
Cardiidae	2	0
Cerianthidae	0	1
Clavelinidae	59	90
Comasteridae	17	5
Conidae	0	1
Diadematidae	0	1
Diazonidae	0	31
Didemnidae	817	545
Diogenidae	3	5
Echinometridae	1	2
Elysiidae	0	1
Flabellinidae	0	1
Halocordylidae	12	0
Majidae	0	1
Ophidiasteridae	1	2
Ophiotrichidae	12	2
Paguridae	19	18
Pectinidae	2	3
Phidoloporidae	0	56
Phyllidiidae	3	0
Plumulariidae	246	186
Polyclinidae	50	0
Pycnoclavellidae	30	224
Sabellidae	4	41
Serpulidae	22	9
Spondylidae	0	1
Stichodactylidae	1	0
Stomachetosellidae	38	9
Styelidae	15	7
Synaptidae	5	0
Zoanthidae	17	2

Table 2. Various diversity indices were calculated and then averaged to counter for the shortcomings of each index which would have a greater impact on the results due to the small sample size. H and S denotes the reefs Hoga and Sampela respectively, with the second letters of: L, M and H indicating the HAS category.

Sample	Family Richness	Margalef	Menhinick	Alpha α	McIntosh U	1/D	H
HL	4	0.8909	0.7427	0.0880	0.8340	0.6956	0.6415
	8	1.6421	0.9494	0.0266	0.6111	0.3735	1.3818
	4	0.8437	0.6761	0.0319	0.6571	0.4318	1.0106
	6	1.1443	0.6750	0.0009	0.7926	0.6282	0.7275
	11	2.1443	1.0684	0.0154	0.6192	0.3834	1.4622
HM	4	0.6807	0.4417	6.18564E-06	0.9516	0.9057	0.2456
	8	1.3114	0.5547	1.91001E-08	0.9095	0.8272	0.4705
	8	1.4807	0.7525	0.0003	0.6544	0.4283	1.1839
	12	1.9186	0.6826	1.46931E-08	0.5821	0.3388	1.4325
	9	1.8894	1.0834	0.0696	0.4516	0.2039	1.8438
HH	6	1.1443	0.6750	0.0009	0.7725	0.5968	0.8630
	7	1.3469	0.7548	0.0018	0.5591	0.3126	1.3965
	7	1.6265	1.1067	0.2713	0.5689	0.3237	1.4751
	6	1.2114	0.7620	0.0088	0.7848	0.6160	0.8348
	3	0.9617	1.0606	1.2521	0.6846	0.4687	0.9002
SL	8	1.6768	0.9922	0.0474	0.5888	0.3467	1.3505
	5	1.1343	0.8574	0.1180	0.5244	0.2750	1.3858
	9	1.9787	1.1920	0.1913	0.6145	0.3776	1.3859
	5	0.9077	0.5521	9.51604E-05	0.8715	0.7596	0.5129
	7	1.2365	0.6187	1.44045E-05	0.7490	0.5610	0.8994
SM	8	1.43360	0.6963	5.63536E-05	0.9101	0.8283	0.4590
	7	1.7159	1.2185	0.5421	0.4143	0.1717	1.8290
	6	1.2534	0.8164	0.0241	0.6241	0.3895	1.1738
	5	0.9809	0.6509	0.0031	0.6657	0.4432	1.0897
	5	1.0918	0.8006	0.0587	0.6582	0.4332	0.9898

Sample	Family Richness	Margalef	Menhinick	Alpha α	McIntosh U	1/D	H
SH	5	1.4770	1.2909	1.3413	0.5849	0.3422	1.2634
	8	1.7893	1.1313	0.1940	0.4841	0.2344	1.6672
	7	1.3145	0.7144	0.0005	0.7518	0.5653	0.8406
	8	1.2714	0.5100	3.31298E-10	0.5829	0.3398	1.2950
	10	1.7867	0.8058	0.0001	0.4834	0.2336	1.6957

The result of the MANOVA with Hotelling's p-value (uncorrected significance) (Wilks' lambda = 0.1587 with F = 1.01 and p= 0.4739 (df1: 40; df2: 76.9); Pillai's trace = 1.374 with F = 0.9949 and p= 0.492 (df1: 40; df2: 105)) was not significant with p-values ranging from 0.828455 – 0.998152. This indicates that there was no significant difference in diversity between either the HAS categories or the reefs.

The Shepard's plot done for the NMMDS scatter plot showed that the Bray-Curtis similarity measure offered the best solution, (Figure 5) with the scatter points following a 1:1 trend the stress value was also relatively small (0.1842) indicating good fit. The NMMDS scatter plot using family abundance in all the replicates in each HAS category and on each reef (Figure 6) shows two mini clusters, 1) HH4, HM1, HM3, SL1; 2) HL4, HL5, SM3; and one less tight cluster of HH2, HM5, HL3, and SM5. To further analyze these clusters the input data for the calculation of the Bray-Curtis similarity measures were simplified to family abundance in each HAS category on each reef. The NMMDS result (Figure 7) delivered by using this input data shows more clear trends under less distortion as the Shepard's plot (Figure 8) has a stress factor of 0 and the scatter points follow a 1:1 trend. It is apparent from the NMMDS scatter plot that the high HAS category on the pristine Hoga reef is more similar to the low HAS category on the same reef than to the high HAS category on the impacted reef, Sampela. Overall the Bray-Curtis similarity measures show a clear distinction between Hoga and Sampela, regardless of HAS category, as the datum points are not plotted close to each other. The cluster analyses (Figure 9) confirms that the high HAS category on Hoga is most similar to the low HAS category on Hoga. The med HAS category on the Hoga reef is the least similar to the other Hoga data sets. The Sampela data are clustered together and are thus seen as similar; although the high HAS category data is less similar to the med and low HAS category data. There is almost the same level of similarity between

the other Sampela categories and Sampela high as there is between Sampela high and Hoga low and high.

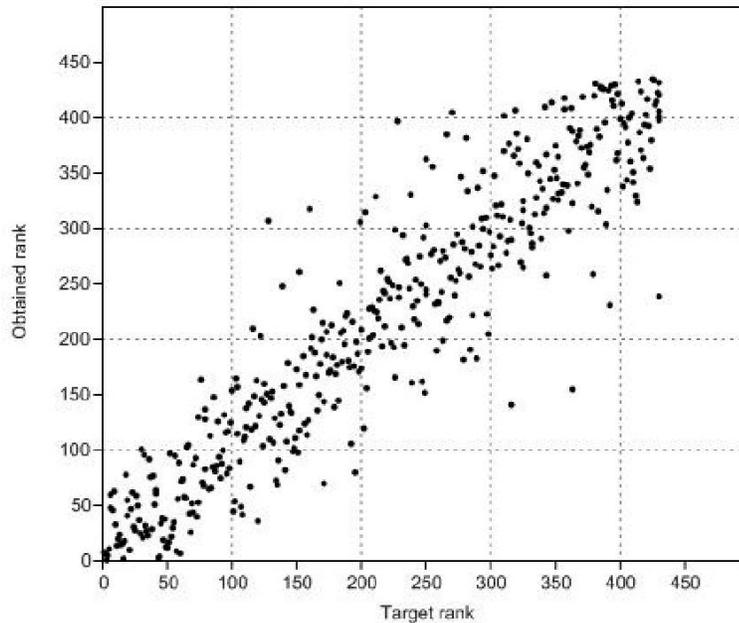


Figure 5. The Shepard's plot done for the NMMDS using the Bray-Curtis similarity measures. The stress factor is a very low 0.1842 and the points follow a general 1:1 trend, which indicates a good fit.

The results of the Sign tests (Table 3) delivered only one significant p-value which was for the comparison of the average diversity per habitat complexity value between Hoga and Sampela for the low HAS category.

Table 3. Results of the Sign test which compared the average diversity per habitat complexity values, between impacted and pristine reef sites for each HAS category.

	p-values	Significant
Hoga High _ Sampela High	0.4531	-
Hoga Med _ Sampela Med	0.4531	-
Hoga Low _ Sampela Low	0.01563	p < 0.05

Discussion

Habitat structural complexity appears to be an important driver of invertebrate diversity on impacted reefs when compared to pristine coral reefs. The structural complexity of coral reefs do not appear to be influenced by depth as is evident from the regression analyses. These findings led to the data collection in phase 2 to be done randomly regardless of depth. The range of HAS on Sampela is surprisingly varied ranging from a very high 27 to a very low 12. The most dominant organisms on the reefs belonged to Didemnidae a family of sea squirts which occurred in clusters on the reefs. The MANOVA results were not significant which indicates that there was not a significant difference in diversity between the samples in each HAS category, between HAS categories on each reef and between the reefs. This result does not meet the expectations: 1) that diversity will increase with an increase in habitat complexity, and 2) that an impacted reef will have less diversity than a pristine reef. Regardless of these results the NMMDS results show that the invertebrate diversity on Sampela and Hoga are not very similar as the Sampela HAS categories are distinguished from the Hoga HAS categories on the scatter plot (Figure 7). The cluster analysis intriguingly reveals the high HAS category on Hoga being most similar to the low HAS category, on the same reef, which is completely contrary to expectation. To add to this the high HAS category of Sampela is almost equally similar to the Hoga low and high categories, as it is to the Sampela low and med HAS categories. It could be that the high habitat complexity on Hoga has reached some threshold, as suggested by Kelaher (2003), past which the increase in habitat complexity has no effect or maybe even a negative effect on the diversity of associated organisms. Kelaher's (2003) results demonstrated distinctive upper thresholds in the association between structural complexity and gastropod species richness. The opposite effect of thresholds has also been mentioned in Witman (1985) where it was observed that the refuge effect on diversity is more effective beyond a habitat complexity threshold. Numerous authors have likewise considered an indirect effect of habitat complexity in: species-area relationships (Hart & Horwitz, 1991; McCoy & Bell, 1991; Huston, 1994), and also in results from studies done in aquatic habitats (Heck *et al.*, 1991; Beck, 1998). Le Hir & Hily (2005) similarly suggest that a threshold effect could explain their less than direct findings between biodiversity and habitat complexity/heterogeneity. They, Le Hir & Hily (2005), proceed to state that heterogeneity of a habitat is not necessarily enhanced by

the complexity thereof, much rather the composition of the heterogeneity is changed. As is evident from my own results and those of Le Hir & Hily (2005) increased habitat complexity and heterogeneity does not necessarily have greater diversity of organisms which contrasts the spatial heterogeneity hypothesis discussed by both Valiela (1995) and Kelaher (2003). When performing the Sign test the only significant result was gained from comparing the average diversity supported per unit of habitat complexity values of the low HAS category on Hoga reef with that of Sampela reef. This result implies that invertebrate diversity relative to habitat complexity (as measured by HAS and classified in the low HAS category) is greater on the impacted reef, Sampela, than on the pristine reef, Hoga. This also suggests that structural complexity may be a more important driver for invertebrate diversity on impacted reefs than on pristine reefs. The observation of this difference might be attributable to the actual HAS values of the categories. The low HAS categories had distinct HAS value ranges, Sampela low HAS category ranging from 12 – 14 and the low HAS category on Hoga ranging from 17 – 18. The ranges from the other categories were consecutive (med HAS category on Sampela 18 – 20 and on Hoga 21 – 23) or overlapping (high HAS category on Sampela 24 – 27 and on Hoga 26 – 28). It could also be that the regular disturbance events on Sampela may generate diversity as suggested by the intermediate disturbance hypothesis (Wilson, 1994), also by Begon, Harper & Townsend (1996), and that the invertebrate community on Sampela is in a continual state of recovery, from the disturbance, through colonization as explained by Pandolfi & Jackson (2007). Patches of low HAS are created by the regular disturbance events (by destroying coral colonies and structurally complex growth forms such as gorgonian sea fans) and it is possible that patch-dynamics are also regulating the reef community on the fragmented Sampela reef. The creation of these gaps is of considerable importance to sessile or sedentary species for which open space is a limiting factor (Begon, Harper & Townsend, 1996). Even though disturbance events cause both habitat fragmentation and loss, both of which have been identified to drive population declines (Bonin, Almany & Jones, 2011), Alvarez-Filip *et al.* (2009) raises the point that on coral reefs habitat area remains even after decreases in live coral cover has occurred, as the reef framework persists long after the coral has died. This is also applicable to my study in the sense that the coral rubble separating intact coral reef patches still provides complexity and refuges for organisms, which could also affect the diversity in the low

HAS samples on Sampela. It should also be mentioned that the low Has samples often contained patches of sand which hosted in-fauna which are not strictly coral reef inhabitants and this might have affected the diversity in these samples.

Even though my results show that the impacted reef supported more diversity per unit of habitat complexity it is not to say that such disturbances should be permitted. Further studies should focus on the amount of disturbance which can be tolerated by the reef communities and the regeneration time necessary for the reef communities. This information could aid conservation in areas where people who have their sole source of income from the reef, by mitigating; managing and limiting these disturbances.

The implications of the influence structural complexity has on diversity could be used in conservation efforts to establish priori areas for conservation and which areas to include in Marine Protected Areas (MPAs). This subject deserves further study, especially in light of the global degradation of reefs such as the flattening of reefs in the Caribbean (Alvarez-Filip *et al.*, 2009) where structural complexity has largely been lost.

Future studies could assess more samples and instead of using HAS categories use the HAS values in and of themselves. It could also be beneficial to include the soft coral and coral species data somehow. This in combination with functional diversity and more analysis of the communities in these areas of various complexities will contribute to a basis from which coral reef conservation issues can be addressed and decisions can be made regarding which features and areas to include in MPAs. The findings of this study could also serve in developing methods for maintaining diversity. In conclusion the findings of my research show that habitat structural complexity is an important driver of invertebrate diversity on Sampela reef when the relative species diversity supported by a comparative unit of habitat complexity is compared to that of Hoga reef. Furthermore my results indicate the presence of an upper complexity threshold on Hoga, the pristine reef.

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