[X]position, Vol. 4, 2019

HOW IMPORTANT IS REEF TYPE IN INFLUENCING THE DIVERSITY AND ABUNDANCE OF INVERTEBRATE AND FISH FEEDING SPECIES GROUPS IN THE TRINCOMALEE BAY AREA?

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(Submitted *April 2019*; Reviewed *June 2019*; Accepted *Sep 2019*)

ABSTRACT

Evaluating the structure of fish assemblages (the number and abundance of different fish species in a given body of water) can be used to assess reef health, environmental quality, and change, which is critical as tropical reefs face unprecedented pressures from human-derived sources. The structure of invertebrate (invertivore) and fish-feeding (piscivore) species groups, called trophic guilds, were assessed in relation to coral and sandstone reef habitat types within the Trincomalee Bay area. Variation in the physical parameters of reef habitats can alter the amount of shelter and food available, influencing the diversity and abundance of reef fish communities. Species richness (number) was positively influenced by several habitat types, while abundance showed no correlation with habitat type and nor did two-way interactions between the guild and habitat type. Diversity of fish assemblages was not correlated with differences in reef habitat type. Observationally, the reef habitat types showed variation in structural complexity, live coral cover, diversity of coral species, and proportion of coral, coral rubble and sandstone. Understanding the physical characteristics of tropical reef habitats that promote diversity and abundance of reef fish assemblages and how fish-habitat interactions influence the structure of these assemblages is critical for the maintenance of ecosystem functioning and the protection of these vulnerable ecosystems. This study not only highlights the fish-habitat interactions on unique sandstone reef habitat types, but also adds to the sparse literature regarding the Trincomalee Bay area and moves towards a better understanding.

INTRODUCTION

Tropical reefs are extremely diverse systems providing shelter and food for a vast range of reef fish species (Chabanet et al., 1997). Disturbance, events or processes that cause displacement or death in reef systems play a key role in maintaining high species diversity, creating new reef patches for settlement (Nyström, Folke and Moberg, 2000). The impact of disturbance on reef organisms is mediated by the physical structure of reef systems (Nyström, Folke and Moberg, 2000). While reef species benefit from physical disturbance, shifting patterns in disturbance from human activities (namely destructive fishing practices and unregulated tourism combined with the effects of climate change) cause degradation of reefs around the world (Nyström, Folke and Moberg, 2000; Cheal *et al.*, 2010). Understanding the processes involved in structuring reef fish communities is essential for their protection and management (Knowlton and Jackson, 2008). Variation in the physical structure of tropical reefs impacts the structure of associated fish assemblages, and is one of several influential processes involved in structuring reef fish assemblages (Öhman and Rajasuriya, 1998). Reef fish associated with reefs for food and protection, with the availability of food and shelter differing between habitat types, influencing the structure of associated fish assemblages (Friedlander and Parrish 1998, Öhman, Rajasuriya and Ólafsson, 1997). Furthermore, fish species distributions are known to be separated by habitat type (Sale, 1991). Hence, distinct features of different habitat types contribute to the diversity and structure of reef fish assemblages. Understanding these is vital for our knowledge of tropical reef systems.

Habitat structure is regarded as one of the most influential factors impacting the abundance, distribution and diversity of fish assemblages (Öhman and Rajasuriya, 1998). Structural complexity, total live coral cover and substratum composition diversity comprising the seafloor (referring to the diversity of coral species and proportion of coral, coral rubble, sand and sandstone) are key physical tropical reef habitat components (Öhman and Rajasuriya, 1998). Structural complexity is accepted as having a positive effect on species diversity and biomass (Öhman and Rajasuriya, 1998; Gratwicke and Speight, 2005). In regard to total abundance, the direction of the effect of structural complexity is less clear, as positive correlations (Grigg, 1994), limited correlations (B. E. Luckhurst and Luckhurst, 1978) and no correlations have been recorded (McClanahan, 1994). Live coral cover can increase species richness and abundances of associated reef fish assemblages (Carpenter *et al.*, 1978; Sano, 2000; Garpe and Öhman, 2003). However, Roberts Ormond (1987) observed no significant correlation between live coral cover and species richness or abundance of fish assemblages. Hence, identifying the most influential factor and understanding its effects on reef fish community composition is challenging (Jackson, 1991; Komyakova, Munday and Jones, 2013).

Almost all available resources on the reef are utilized by reef fish; hence, reef fish play an important role in reef ecosystem dynamics (Kramer *et al.*, 2015). A guild is a group of species that utilize similar resources in a common manner . Fish species within an assemblage can be grouped into different trophic guilds depending on the food resources they exploit. Invertivore fish feed solely on invertebrates (mainly crustaceans) and are highly abundant on coral reefs (Prog, Williams and Hatcher,

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1983). Crustaceans play an important role in food webs, forming a key link between primary production and consumers. Hence, the invertivore trophic guild is a key component of reef ecosystems (Kramer *et al.*, 2015). Piscivorous fish are characteristically carnivorous and prey on a wide variety of fish species, having a stabilising effect in aquatic systems through predation on lower trophic levels (Boaden and Kingsford, 2015). Boaden and Kingsford (2015) proposed evidence supporting the function of piscivorous fish in structuring coral reef assemblages in maintaining an abundance of lower trophic level species. Overall, invertivore and piscivore trophic guilds are a key component of reef fish assemblages and, thus, their removal can negatively affect reef communities.

Compared to coral reefs, there are fewer studies focusing on sandstone reefs, which are only found extensively in Brazil (Soares *et al.*, 2017) and Sri Lanka (Öhman, Rajasuriya and Ólafsson, 1997; Öhman and Rajasuriya, 1998). The Trincomalee Bay area is unique in that coral and sandstone reefs are found in close proximity, sometimes even interchanging across sites, thus presenting a valuable opportunity to investigate the effect of coral and sandstone reefs on the structure of the invertivore and piscivore trophic guilds. This study will not only shed light on the fish-habitat interactions of sandstone reefs, but will also add to the sparse literature on the region as previous studies on the sandstone reefs of Sri Lanka are concentrated on the North-western side of the island (Öhman, Rajasuriya and Ólafsson, 1997; Öhman and Rajasuriya, 1998). Evaluating the structure of fish assemblages can be used to assess reef health, environmental quality, and change (Stephens, Hose and Love, 1988; Brokovich, Baranes and Goren, 2006). This is increasingly important as tropical reefs the world over face unprecedented pressures from human-derived sources. The purpose of this study was to produce a solid baseline data set of the diversity and abundance of the invertivore and piscivore trophic guilds in the Trincomalee Bay area. This can be built upon and used to monitor reef health and ecological change as currently there is no such program in place. This is critical if there is another mass-bleaching event such as the one in 1998, as community data will exist before its occurrence, allowing the ecological impact of the event to be quantified (Sheppard, 2003).

This study aims to examine the diversity and abundance of the invertivore and piscivore trophic guilds across 14 sites in the Trincomalee Bay area by sampling reef habitats. It is expected that the abundance and distribution of species from the invertivore and piscivore trophic guilds will differ across the 14 sample sites. Defined fish assemblages for each distinct reef habitat type (coral and sandstone) are expected. However, as these sites represent a continuum of habitat types, it may be difficult to observe distinct fish assemblages between the sampled habitats; regardless, variation should be detected. Overall, this study will provide an insight into how differences in benthic habitat impact the structure of associated fish assemblages.

METHODS

A transect is a given length of measuring tape used to mark a line across a habitat (a 'transverse section') and record the species present along with their abundance. 20m by 5m visual belt transects were carried out in the Trincomalee Bay area to assess the invertivore (insect-eating) and piscivore (fish-eating) fish trophic guilds across a variety of coral and sandstone reef habitat types. Fourteen sites were haphazardly sampled, subject to permit and boat limitations, from the 24 June 2018 to the 22 July 2018, totalling 24 dive days and amounting to 140 transects. A typical sampling day included two dives at one site with three transects completed per dive.

The sites in Figure 1 were haphazardly sampled using a list of bearings and fin kick cycles (diver kicks once with each leg) that were randomly generated using an online random number generator prior to the dive to locate transect starting points. The sites were sampled using a four-man dive team consisting of two buddy teams. The first buddy pair consisted of two fish observers who recorded the abundance of fish from the invertivore and piscivore trophic guilds, while the second buddy pair recorded habitat type and unwound the transect reel.

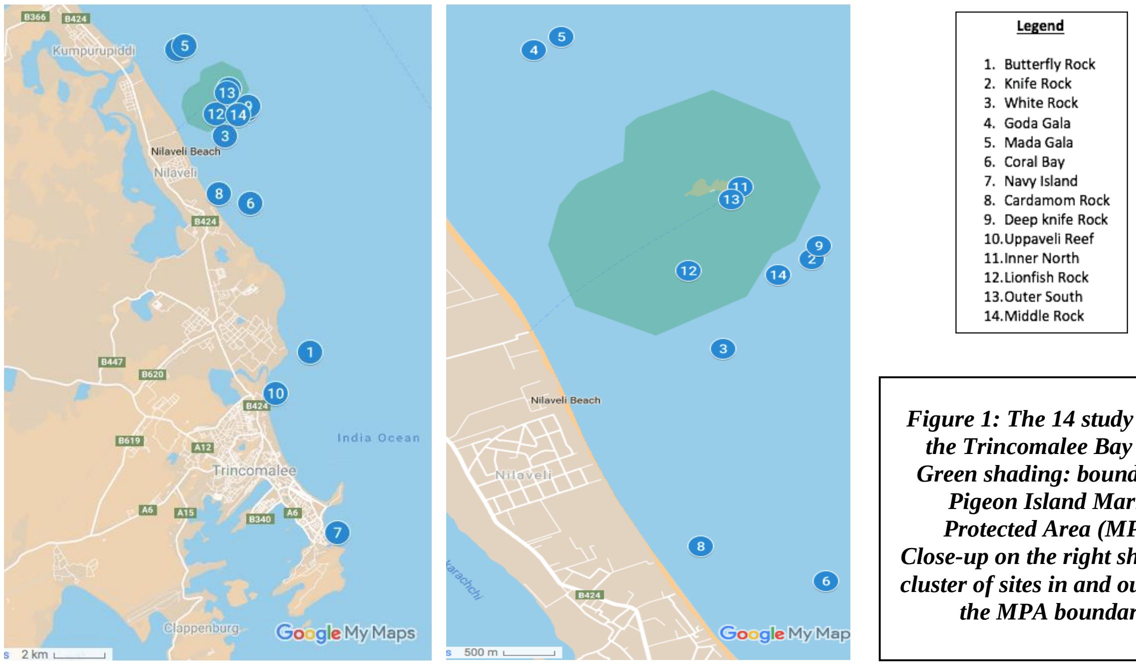

Figure 1: The 14 study sites in the Trincomalee Bay area. Green shading: boundary of Pigeon Island Marine Protected Area (MPA). Close-up on the right shows the cluster of sites in and outside of the MPA boundary.

Figure 2 outlines the positioning of the 4-man dive team and the visual boundary of the survey.

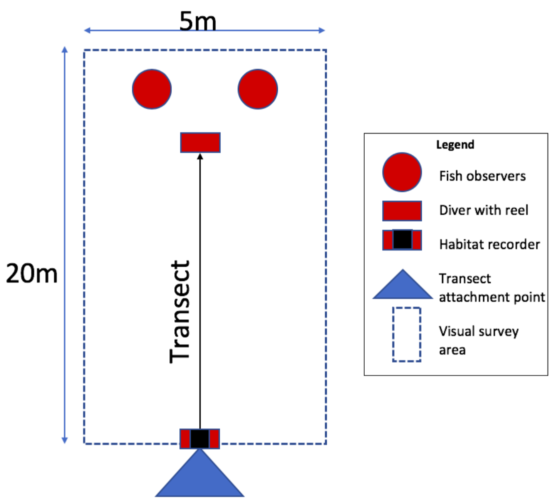

Figure 2: Positioning of the four-man dive team and the visual boundary of the survey.

Definitions Of Reef Habitat Types

Due to the large number of habitat combinations, they were grouped into habitat substratum categories: *combination*, *coral* and *sandstone* (Table 2). The *combination* category represents transects where two or more habitat types of different substratum were encountered. The habitat types were found discreetly or combined across transects, forming 15 different habitat types and combinations.

Statistical Analyses

Species richness, Shannon's Diversity Index, and Simpson's Diversity Index (measures of how many different species are present in a sample) were calculated for each transect. To test the effect of habitat substratum and type on the structure of the invertivore and piscivore trophic guilds, a statistical test was carried out. The smaller the value produced, the less likely the result was obtained by chance. If a p-value of < 0.05 was returned, the result was deemed to be statistically significant. Additional analyses were used to confirm further, and to differentiate between which habitat substratum or type the significant difference occurred.

Table 2: Definitions of the coral and sandstone reef habitat types identified during pilot dives and defined by Ohman et al (1995)

Reef substrate	Reef habitat type	Description
Sandstone	Structured	Consists of rocky sandstone substrate which rises off the substratum causing a structured reef with significant topographic relief. Patches are characterised by rocks and small hills as well as fragmented plateau-like structures with holes and crevices.
	Flat	Consists of rocky sandstone substrate which rises off the substratum to a lesser extent than structured sandstone. This habitat type lacks prominent features and mainly contained flat slab like rocks.
Coral	Patch	Several coral species tightly grouped together forming a coral patch.
	Flat	Large flat patches of coral, typically containing branching Acropora stands.
	Rubble	Various levels of coral degradation, loss of coral structural integrity and often algae growing on rubble pieces.
Sand	Sand	Extending patches of sand only.

RESULTS

A total of 2529 individuals comprised of 46 species from 10 families of fish were recorded on coral and sandstone reef habitat types. Sampling took place over 14 sites, representing six distinct habitats. Structured sandstone was the most sampled habitat type, with 65 transects, while flat coral was only encountered on two transects. The highest species richness per transect was 11, recorded on structured sandstone at Moda Gala. Table 3 summarises the invertivore and piscivore guilds encountered in this study.

Effect Of Habitat Substratum and Habitat Type on Species Richness Of Invertivore and Piscivore Trophic Guilds Combined

No significant difference in species richness was detected between the three habitat substrata: combination, coral and sandstone (Figure 3a). The combination and sandstone substratum categories had the highest median species richness (median = 5 and 5) while the coral category had the lowest (median = 3).

Figures 3b, 3c and 3d illustrate the variation in species richness of the habitat types contained within each of the substrata categories presented in Figure 3a.

Figure 3b shows the eight habitat type combinations encountered. Species richness varied considerably across the habitat type combinations, with structured sandstone/coral rubble having the highest species richness, compared to the lowest observed on flat sandstone/flat coral/sand and patch coral/sand (median = 7 and 3, respectively). No significant difference was detected in species richness between the combination substrata categories.

Species richness on flat coral/coral rubble, and on patch coral/coral rubble, was significantly higher than on coral rubble alone. Further analyses confirmed this finding.

In the sandstone substrata category, structured sandstone had the highest species richness (median = 6). Structured sandstone had a significantly higher species richness than flat sandstone. There was no significant difference between structured sandstone and flat sandstone/structured sandstone, or between flat sandstone and flat sandstone/structured sandstone.

Effect of Habitat Types Sampled More Than Five Times on the Species Richness, Shannon's Diversity, and Simpson's Diversity of the Invertivore and Piscivore Trophic Guilds Combined

Due to the large number of habitat types with few observations, habitat types sampled fewer than five times were removed.

Patch coral/coral rubble and structured sandstone had significantly higher richnesses than coral rubble (Figure 4a).

Further analyses confirmed this, and that structured sandstone had a significantly elevated species richness compared to flat sandstone. No other significant differences in species richness between habitat types were detected.

No significant differences in Shannon's Diversity Index were detected. Structured sandstone had the highest median Shannon's Diversity Index, while structured sandstone/flat sandstone had the lowest (median = 1.43 and 0.56, respectively) (Figure 4b).

Structured sandstone had the highest median Simpson's Diversity, while structured sandstone/flat sandstone had the lowest (median = 0.71 and 0.38, respectively) (Figure 4c). No significant differences in Simpson's diversity were detected.

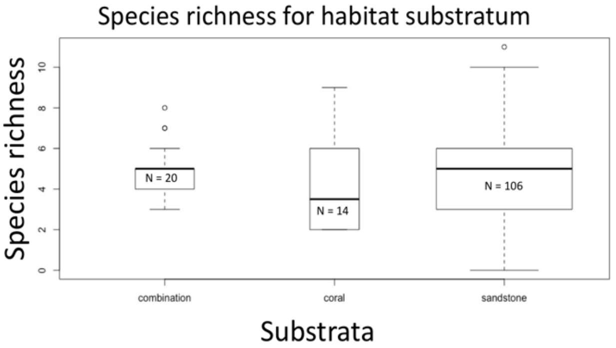

Figure 3a: Species richness for each habitat substratum category: combination, coral and sandstone.

***The median, represented by a black line, and 50% of the data points lie within each box. The whiskers extend above and below the box to the lowest and highest values but do not extend beyond 1.5*Inter quartile range (IQR). Black circles represent individual outliers which lie out with this range. Sample size for each habitat type is denoted by* N.**

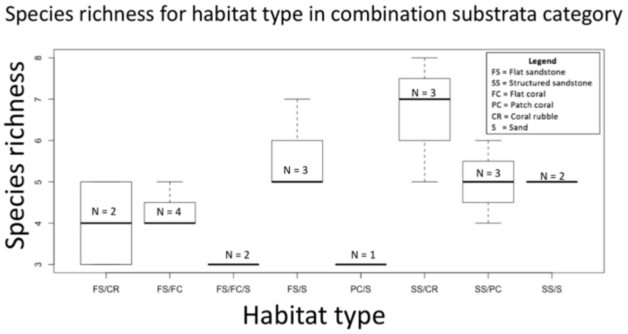

Figure 3b: Species richness for habitat types within the 'combination' category

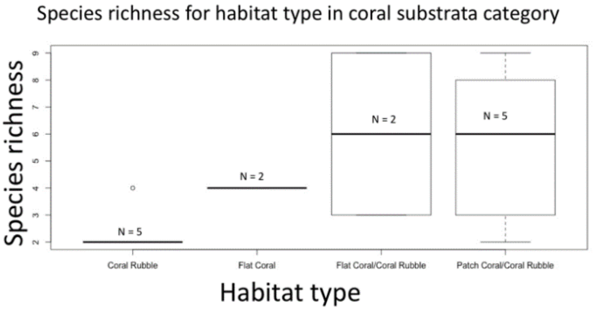

Figure 3c: Species richness for habitat types within the 'coral' category

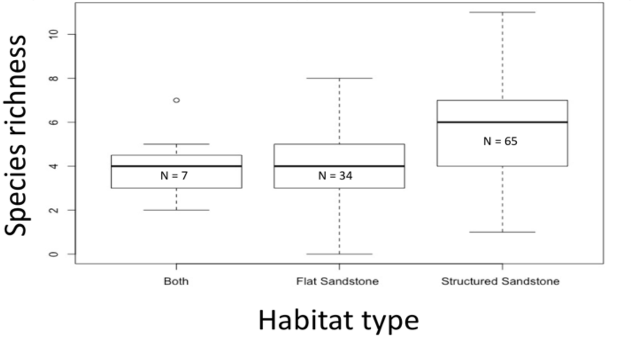

Figure 3d: Species richness for habitat types within the 'sandstone' category

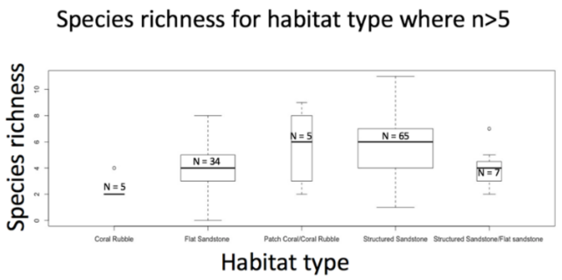

*Figure 4a: Species richness for habitat types that were sampled more than five times. The median, represented by a black line, and 50% of the data points lie within each box. The whiskers extend above and below the box to the lowest and highest values but do not extend beyond 1.5*Inter quartile range (IQR). Black circles represent individual outliers which lie out with this range. Sample size for each habitat type is denoted by N.*

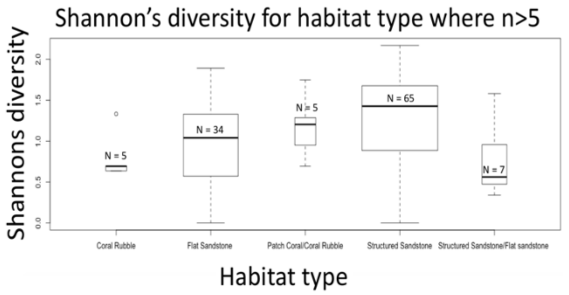

Figure 4b: Shannon's diversity for habitat types that were sampled more than five times.

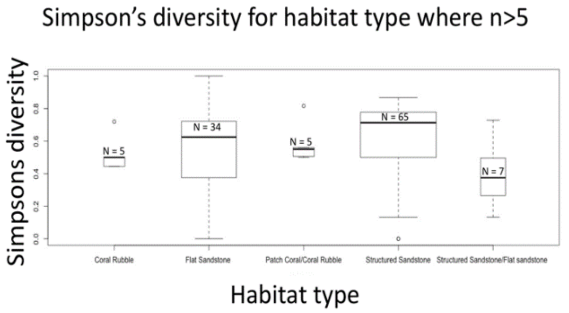

Figure 4c: Simpson's diversity for habitat types that were sampled more than five times.

Effect of Habitat Types Sampled More Than Five Times on the Number of Individuals Observed in the Invertivore and Piscivore Guilds

Figure 5 highlights the number of individuals in each trophic guild in habitat types that were sampled more than five times. Patch coral/coral rubble had the highest median number of invertivorous fish, while structured/flat sandstone had the lowest (median = 5 and 1, respectively). This guild maintained a consistent number of individuals across all habitats, and also had the lowest total abundance across these five habitat types (n=514). The highest median number of individuals from the invertivore/piscivore trophic guild was found on structured sandstone/flat sandstone (median = 3). The greatest number of individuals on a single transect were observed on structured sandstone (n = 101) while only one fish was observed on coral rubble. The piscivore guild was the most abundant guild (n = 1,172). The highest median number of piscivores was observed on combined structured sandstone/flat sandstone (median = 8). Although piscivores were most frequently detected on sandstone reef habitat, no significant differences in abundance were detected between habitat types sampled more than five times.

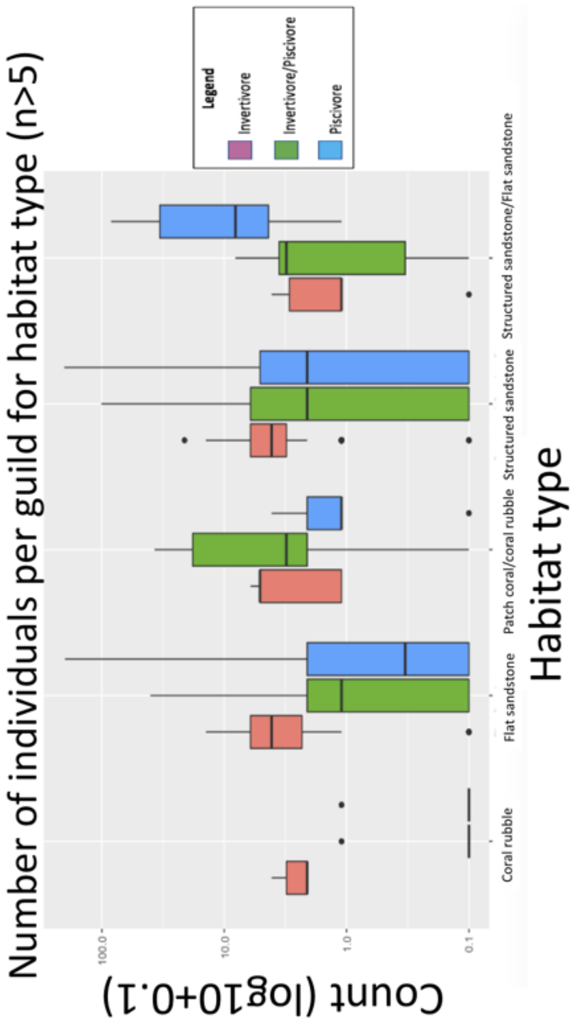

*Figure 5: Number of individuals from the invertivore and piscivore trophic guilds observed on habitat types that were sampled more than five times. The y-axis has been log transformed, hence, 0 = 0.1 to avoid log zero. The median, represented by a black line, and 50% of the data points lie within each box. The whiskers extend above and below the box to the lowest and highest values but do not extend beyond 1.5*Inter quartile range (IQR). Black circles represent individual outliers which lie out with this range. Sample size for each habitat type is denoted by N.*

Structured sandstone had the highest species richness, total abundance, Shannon's Diversity Index and Simpson's Diversity Index (6, 1420, 1.28 and 0.62, respectively) (Table 3) with the majority of fish sampled from the piscivore trophic guild (43.5%). Coral rubble had the lowest species richness and total abundance (2 and 15, respectively) with its fish assemblage comprising mainly of invertivorous fish (86.7%). Structured sandstone/flat sandstone had the lowest Shannon's and Simpson's Diversities (0.76 and 0.39, respectively) (Table 3) with the majority of fish sampled from the piscivore trophic guild.

Table 3: Percentage of each trophic guild, mean species richness, total abundance, mean Shannon's and mean Simpson's Diversity Indices observed on habitat types sampled more than five times.

Habitat type	Invertivore (%)	Invertivore / Piscivore (%)	Piscivore (%)	Mean Species Richness	Total Fish Abundance	Mean Shannon's Index	Mean Simpson's Index
Coral Rubble	86.7	6.7	6.7	2	15	0.80	0.52
Flat Sandstone	25.9	14.3	59.8	4	587	0.99	0.56
Patch Coral/Coral Rubble	20.9	69.8	9.3	6	86	1.18	0.59
Structured Sandstone	23.3	33.2	43.5	6	1420	1.28	0.62
Structured Sandstone/Flat Sandstone	5.7	8.3	86.0	4	228	0.76	0.39

DISCUSSION

As expected, the structure of the fish assemblages across the fourteen study sites differed due to differences in the reef habitats. No significant relationship was detected between habitat substratum and species richness, although when habitat substratum categories were analysed separately, flat coral/coral rubble, patch coral/coral rubble and structured sandstone were correlated with higher species richness. Shannon's and Simpson's Diversity Index were not correlated with habitat type. The total abundance of trophic guilds showed no significant differences, nor were interactions between guild, total abundance and habitat type detected. Differences in benthic habitat did affect the species richness of associated fish assemblages, but did not exhibit any significant influence on the structure of the invertivore and piscivore trophic guilds. Understanding the physical characteristics of tropical reef habitats that promote diversity and abundance of reef fish assemblages and the way fish-habitat interactions influence the structure of these assemblages is critical for the protection of these vulnerable ecosystems.

Few significant differences in species richness were detected, and the influence of habitat type on the structure of the invertivore and piscivore trophic guilds was difficult to deduce. The small sample sizes of many of the habitat types made it difficult to draw conclusions and reliably detect differences in the structure of fish assemblages. When two or more habitat types were encountered on one transect, they were collectively recorded as one habitat type, thus likely influencing the results. Habitat type was determined visually, and habitat and fish recording were only done by a select few individuals to minimise inconsistencies. In general visual census, methods undervalue true populations, especially of very abundant and cryptic species (Fowler, 1987; Chabanet *et al.*, 1997; Thompson and Mapstone, 1997). Regardless of the limitations of this study, the results provide valuable insight into the role of habitat type in structuring invertebrate (invertivore) and fish feeding (piscivore) species groups (trophic guilds), which is vital for protecting the future of tropical reef ecosystems.

Effect of Benthic Habitat on Species Richness and Diversity of Fish Assemblages

No relationship between habitat substratum categories or combinations of two or more habitat types and species richness was observed. Besides the issues regarding sample sizes, the habitat itself may have impacted the results. Coral rubble and sand were present in six of the eight habitat combinations. Coral rubble is broken decaying coral. Having lost its structural integrity, it affords minimal protection, much like expanses of sand where fish abundance is generally low (Carpenter *et al.*, 1978). Anecdotally, these habitat types lacked structural complexity and substratum composition diversity, likely resulting in the lower species richnesses observed (Öhman, Rajasuriya and Ólafsson, 1997; Pierre and Kovalenko, 2014).

Interestingly, when habitat types within the coral and sandstone substratum categories were analysed separately, clear trends were highlighted.

Species richness was positively correlated with flat coral/coral rubble and patch coral/coral rubble. Observationally, flat and patch coral appeared more structurally complex, which is correlated with heightened species richness in several studies (Roberts and Ormond, 1987; Chabanet *et al.*, 1997). Increasing structural complexity provides a greater variety of refuges for a wider array of reef fish species (Friedlander and Parrish, 1998). Although coral rubble was found in the above habitat types, the presence of flat and patch coral habitat types may have had a large effect on species richness. Coral rubble may not degrade species richness as heavily as assumed, since the live coral cover is not always correlated with species richness (B. E. Luckhurst and Luckhurst, 1978; Roberts and Ormond, 1987). Furthermore, coral rubble has been shown to support different fish assemblages compared to other reef habitat types, such as patch coral (Kendall and Miller, 2010). However, in this study, fish assemblages sampled on coral rubble were of low species richness, supporting the results obtained by Öhman and Rajasuriya (1998).

Flat coral was characterized by large expanses of branching coral, namely *Acropora*, exhibiting low coral species diversity. This likely restricted fish species richness as the diversity of substrate types has been positively correlated with species richness (Öhman and Rajasuriya, 1998). The influence of single species *Acropora* stands on species richness is conflicting, as branching coral exhibits high structural complexity (Chabanet *et al.*, 1997) which has been linked with inflated species richness (B. E. Luckhurst and Luckhurst, 1978; Friedlander and Parrish, 1998; Öhman and Rajasuriya, 1998). The heightened structural complexity of branching coral appears to counteract the expected effect of low substratum composition diversity observed on flat coral due to expanses of a single coral species. This demonstrates the important role of the structural complexity of coral habitat types on the diversity of fish assemblages.

On coral reefs, fish rely on the substrate for food and shelter, impacting fish diversity and abundance (E. Luckhurst and Luckhurst, 1978; Friedlander and Parrish, 1998). Few studies have examined fish-habitat interactions on sandstone reefs (Öhman and Rajasuriya, 1998). Fish assemblages on sandstone reefs are likely influenced by similar processes to those on coral reefs such as substratum composition diversity, habitat complexity and live coral cover (E. Luckhurst and Luckhurst, 1978; Friedlander and Parrish, 1998; Öhman and Rajasuriya, 1998). The current study found that structured sandstone positively influenced species richness. The higher species richness of fish assemblages observed on structured sandstone compared to flat sandstone is in concordance with the results observed by Öhman and Rajasuriya (1998). Anecdotally, flat sandstone did not exhibit the same structural heterogeneity as structured sandstone providing less refuge sites for residing reef fish and fewer microhabitats which in turn reduces the number of species supported by that habitat (Friedlander and Parrish, 1998; Graham and Nash, 2013; Shulman, 1984). Thus, the amount of refuge and food provided by a habitat type is an important factor affecting species diversity.

Species richness was also significantly higher on patch coral/coral rubble and structured sandstone when compared to coral rubble. Structured sandstone had the highest recorded species richness of the habitat types, which observationally, was the most heterogeneous habitat type. This is supported by a study showing that high reef structural complexity allows more species to share the same space (Chabanet *et al.*, 1997). Anecdotally, patch coral/coral rubble had a greater substratum composition diversity than coral. Species richness was positively correlated with structural complexity and substratum composition diversity by Öhman and Rajasuriya (1998). These results further highlight the importance of structural complexity and substratum composition diversity on the diversity of fish assemblages.

Shannon’s and Simpson’s Diversity Indices were not correlated with habitat type. Fish associated with particular physical aspects of habitat hence, variation in the diversity of fish assemblages across different habitat types was expected (Sale, 1991; Garpe and Öhman, 2003). Patch coral/coral rubble and structured sandstone had the same species richness and similar diversity values but differed in the percentage composition of the trophic guilds, especially in respect to invertivore/piscivore and piscivore trophic guilds. Although no significant differences in diversity between habitat types were identified, the use of diversity indices in conjunction with species composition helps to highlight the influence of different habitat types on the structure of fish assemblages.

The Trincomalee Bay area likely represents a habitat continuum as coral and sandstone reef habitat types interchanged across the sampled sites, possibly owing to the lack of significant results. Kendall and Miller (2010) experienced this in their study, expressing that different reef habitat types can share similar physical characteristics. A certain degree of overlap in fish assemblages is to be expected as the spatial separation between sample sites was not sufficient to exclude the possibility of migration between sites (Kendall and Miller, 2010). Overall, the lack of significant differences in species richness and diversity between habitat types is likely a result of a continuation of fish assemblages across the sampled habitat types.

Effect of Benthic Habitat on the Structure of the Invertivore and Piscivore Trophic Guilds

The effect of habitat type on the number of individuals in each trophic guild was not correlated, nor was a relationship with total abundance detected. Uneven distribution of the invertivore and piscivore guilds was observed across reef habitat types, supporting the findings of Öhman, Rajasuriya and Ólafsson (1997). The food and shelter requirements of invertivore and piscivore guilds differ; thus, distributions were expected to vary across habitat types (Öhman, Rajasuriya and Ólafsson, 1997). The invertivore guild was the least abundant across the five habitat types, but it was also the most consistently encountered guild with one to eight individuals recorded on every transect. Of the 46 species on the fish list utilised in this study, 25 species belonged to the invertivore guild, possibly accounting for its consistent appearance on all transects. Coral rubble had the lowest species richness and total abundance of any sampled habitat, likely due to coral rubble lacking structural complexity which has been correlated with a lower number of benthic invertebrates (Öhman, Rajasuriya and Ólafsson, 1997). Despite this lack of food, the invertivore guild comprised 86.7% of the fish sampled on coral rubble, but compared to the other habitat types it was sparsely populated. Although the invertivore and piscivore trophic guilds differ in their food and shelter requirements, no significant differences in guild structure was observed in regard to habitat type.

The invertivore/piscivore guild is comprised of species that feed on both fish and invertebrates. On the sandstone reef habitats, the distribution of their numbers closely matched that of fish feeding species. The piscivore guild was the most abundant in this study and composed a large proportion of the fish assemblages sampled on flat sandstone and structured sandstone/flat sandstone. As mentioned anecdotally, structured sandstone appeared structurally complex compared to the other habitat types. Members from the piscivore guild were sparsely found on coral rubble and patch coral/coral rubble. Species richness and total abundance on coral rubble were very low, thus there would have been few fish for piscivores to prey on. Öhman and Rajasuriya (1998) observed a correlation between structural complexity and fish and invertebrate feeders on sandstone reefs. Differences in food availability between the two habitat types could explain why the piscivore guild was so abundant on some structured sandstone transects but less so on coral rubble. Predatory fish are important regulators of prey abundances and keep numbers within the carrying capacity of the system (Stewart and Melbourne, 1998). Observing high numbers of piscivores could be acknowledged as a positive indication of the health of fish assemblages in the Trincomalee Bay area.

Understanding the role of benthic habitat in structuring reef fish assemblages goes far beyond the locale examined in this study. An appreciation of the mechanisms driving abundance and diversity of fish assemblages is vital for preserving the high level of biodiversity on tropical reefs globally. Retaining high species biodiversity is crucial for maintaining ecosystem function (Moberg and Folke, 1999; Pratchett *et al.*, 2016), as high species diversity increases the likelihood of other species being present that can fulfil the same role within the ecosystem as previously present species, maintaining the health of the ecosystem following species loss from disturbances (Pratchett *et al.*, 2016). This is of great importance as coral reefs face increasing pressures from ocean acidification, rising sea temperatures and coral bleaching (Cheal *et al.*, 2010; Pratchett *et al.*, 2016). Identifying and protecting benthic habitats with high levels of structural complexity, live coral cover and substratum composition diversity could help to preserve the high species diversity, in turn safeguarding the invaluable ecosystem functions provided by tropical reefs the world over.

This study has produced a solid baseline data set of the abundance and diversity of the invertivore and piscivore trophic guilds. By adding a measure of habitat structure, variation within habitat types could be compared, and the role habitat structure plays in influencing fish assemblages could be assessed more thoroughly. Due to the haphazard sampling method employed, flat coral and patch coral were sparsely sampled, making inferences on their influence on the structure of fish assemblages unfeasible, thus representing regions of interest to pursue in future work.

CONCLUSION

This study examines how different reef habitat types influence the structure of the invertivore and piscivore guilds. No correlations between reef habitat type and trophic guilds were observed; however, species richness of fish assemblages was positively influenced by structured sandstone, patch coral/coral rubble and flat coral/coral rubble. The consensus on the effect of habitat and its physical parameters on the structure of fish assemblages is widely debated. Anecdotally, variation in the structural complexity and substratum composition of coral and sandstone reef habitats appears to be essential in maintaining high species diversity. Thus, this study identifies physical reef characteristics that should be considered when allocating conservation and protection measures in tropical reef habitats. Fish assemblages are influenced by reef habitat type but determining the most influential physical aspect of habitat in structuring reef fish assemblages is still to be achieved. As human disturbance continues to increase understanding, the key physical factors of reef habitats that promote diversity and abundance of fish communities is vital in order to safeguard these precious ecosystems for future generations.

ACKNOWLEDGEMENTS

I would like to thank University of Glasgow Sri Lanka Expedition 2018 team, Dr Deborah McNeil, Poseidon Diving Sri Lanka, and all organisations and trusts that helped fund this study. Special thanks must be given to my supervisor Dr Donald Reid for his continued support, encouragement and advice. I would also like to thank my two mentors, Sonya Frazier and Cairistiona Russel, for their guidance and feedback throughout the publishing process.

REFERENCES

Boaden, A. E. and Kingsford, M. (2015) ‘Predators drive community structure in coral reef fish assemblages’, *Ecosphere*. John Wiley & Sons, Ltd, 6(4), p. art46. doi: 10.1890/ES14-00292.1.

Brokovich, E., Baranes, A. and Goren, M. (2006) ‘Habitat structure determines coral reef fish assemblages at the northern tip of the Red Sea’, *Ecological Indicators*, 6(3), pp. 494–507. doi: 10.1016/j.ecolind.2005.07.002.

Carpenter, K.E., Miclat, R.I., Albaladejo, V.D., and Corpuz, V.T. (1978) ‘The influence of substrate structure on the local abundance and diversity of Philippine reef fishes’, *nsgl.gso.uri.edu*, 2(16), pp. 1–17. Available at: http://nsgl.gso.uri.edu/hawau/hawauwr81001.pdf (Accessed: 9 January 2019).

Chabanet, P., Ralambondrainy, H., Amanieu, M., Faure, G., and Galzin, R. (1997) ‘Relationships between coral reef substrata and fish’, *Coral Reefs*, 16(2), pp. 93–102. doi: 10.1007/s003380050063.

Cheal, A.J.; MacNeil, M.A., Cripps, E., Emslie, M.J., Jonker, M., Schaffelke, B., and Sweatman, H. (2010) ‘Coral–macroalgal phase shifts or reef resilience: links with diversity and functional roles of herbivorous fishes on the Great Barrier Reef’, *Coral Reefs*. Springer-Verlag, 29(4), pp. 1005–1015. doi: 10.1007/s00338-010-0661-y.

Fowler, A. J. (1987) ‘The development of sampling strategies for population studies of coral reef fishes. A case study’, *Coral Reefs*. Available at: https://link.springer.com/content/pdf/10.1007%2FBF00302212.pdf (Accessed: 14 January 2019).

Friedlander, A. M. and Parrish, J. D. (1998) ‘Habitat characteristics affecting fish assemblages on a Hawaiian coral reef’, *Journal of Experimental Marine Biology and Ecology*, 224(1), pp. 1–30. doi: 10.1016/S0022-0981(97)00164-0.

Garpe, K. C. and Öhman, M. C. (2003) ‘Coral and fish distribution patterns in Mafia Island Marine Park, Tanzania: fish–habitat interactions’, *Hydrobiologia*. Kluwer Academic Publishers, 498(1/3), pp. 191–211. doi: 10.1023/A:1026217201408.

Graham, N. A. J. and Nash, K. L. (2013) ‘The importance of structural complexity in coral reef ecosystems’, *Coral Reefs*, 32(2), pp. 315–326. doi: 10.1007/s00338-012-0984-y.

Gratwicke, B. and Speight, M. R. (2005) ‘The relationship between fish species richness, abundance and habitat complexity in a range of shallow tropical marine habitats’, *Journal of Fish Biology*. John Wiley & Sons, Ltd (10.1111), 66(3), pp. 650–667. doi: 10.1111/j.0022-1112.2005.00629.x.

Grigg, R. (1994) ‘Effects of sewage discharge, fishing pressure and habitat complexity on coral ecosystems and reef fishes in Hawaii’, *Marine*

Ecology Progress Series, 104, pp. 25–34. doi: 10.3354/meps104025.

Jackson, J. B. C. (1991) 'Adaptation and Diversity of Reef Corals', *BioScience*. Oxford University Press, 41(7), pp. 475–482. doi: 10.2307/1311805.

Kendall, M. S. and Miller, T. J. (2010) 'Relationships among map resolution, fish assemblages, and habitat variables in a coral reef ecosystem', *Hydrobiologia*. Springer Netherlands, 637(1), pp. 101–119. doi: 10.1007/s10750-009-9988-1.

Knowlton, N. and Jackson, J. B. C. (2008) 'Shifting Baselines, Local Impacts, and Global Change on Coral Reefs', *PLoS Biology*. Public Library of Science, 6(2), p. e54. doi: 10.1371/journal.pbio.0060054.

Komyakova, V., Munday, P. L. and Jones, G. P. (2013) 'Relative Importance of Coral Cover, Habitat Complexity and Diversity in Determining the Structure of Reef Fish Communities', *PLoS ONE*. Edited by J. Chave, 8(12), p. e83178. doi: 10.1371/journal.pone.0083178.

Kramer, M.J., Bellwood, O., Fulton, C.J., and Bellwood, D.R. (2015) 'Refining the invertivore: diversity and specialisation in fish predation on coral reef crustaceans', *Marine Biology*. Springer Berlin Heidelberg, 162(9), pp. 1779–1786. doi: 10.1007/s00227-015-2710-0.

Luckhurst, B. E. and Luckhurst, K. (1978) 'Analysis of the influence of substrate variables on coral reef fish communities', *Marine Biology*, 49(4), pp. 317–323. doi: 10.1007/BF00455026.

Luckhurst, E. and Luckhurst, K. (1978) 'Analysis of the Influence of Substrate Variables on Coral Reef Fish Communities', *Marine Biology*. Available at: https://link.springer.com/content/pdf/10.1007%2FBF00455026.pdf (Accessed: 9 January 2019).

McClanahan, T. R. (1994) 'Kenyan coral reef lagoon fish: effects of fishing, substrate complexity, and sea urchins', *Coral Reefs*. Springer-Verlag, 13(4), pp. 231–241. doi: 10.1007/BF00303637.

Moberg, F. and Folke, C. (1999) 'Ecological goods and services of coral reef ecosystems', *Ecological Economics*. Elsevier, 29(2), pp. 215–233. doi: 10.1016/S0921-8009(99)00009-9.

Nyström, M., Folke, C. and Moberg, F. (2000) 'Coral reef disturbance and resilience in a human-dominated environment', *Trends in Ecology & Evolution*. Elsevier Current Trends, 15(10), pp. 413–417. doi: 10.1016/S0169-5347(00)01948-0.

Öhman, M. C. and Rajasuriya, A. (1998) 'Relationships between habitat structure and fish communities on coral and sandstone reefs', *Environmental Biology of Fishes*. Kluwer Academic Publishers, 53(1), pp. 19–31. doi: 10.1023/A:1007445226928.

Öhman, M. C., Rajasuriya, A. and Ólafsson, E. (1997) 'Reef fish assemblages in north-western Sri Lanka: distribution patterns and influences of fishing practises', *Environmental Biology of Fishes*. Kluwer Academic Publishers, 49(1), pp. 45–61. doi: 10.1023/A:1007309230416.

Pierre, J. I. S. and Kovalenko, K. E. (2014) 'Effect of habitat complexity attributes on species richness'. doi: 10.1890/ES13-00323.1.

Pratchett, M.S., Hoey, A.S., Wilson, S.K., and Messmer, V. (2016) 'Changes in Biodiversity and Functioning of Reef Fish Assemblages following Coral Bleaching and Coral Loss', 3, pp. 424–452. doi: 10.3390/d3030424.

Prog, S., Williams, D. M. and Hatcher, A. I. (1983) 'Structure of Fish Communities on Outer Slopes of Inshore, Mid-Shelf and Outer Shelf Reefs of the Great Barrier Reef', *Marine Ecology Press Series*. Available at: https://www.int-res.com/articles/meps/10/m010p239.pdf (Accessed: 10 January 2019).

Roberts, C. and Ormond, R. (1987) 'Habitat complexity and coral reef fish diversity and abundance on Red Sea fringing reefs', *Marine Ecology Progress Series*, 41, pp. 1–8. doi: 10.3354/meps041001.

Sale, P. F. (1991) 'Habitat structure and recruitment in coral reef fishes', in *Habitat Structure*. Dordrecht: Springer Netherlands, pp. 197–210. doi: 10.1007/978-94-011-3076-9_10.

Sano, M. (2000) 'Stability of reef fish assemblages:responses to coral recovery after catastrophic predation by Acanthaster planci', *Marine Ecology Progress Series*, 198, pp. 121–130. doi: 10.3354/meps198121.

Sheppard, C. R. C. (2003) 'Predicted recurrences of mass coral mortality in the Indian Ocean', *Nature*. Nature Publishing Group, 425(6955), pp. 294–297. doi: 10.1038/nature01987.

Shulman', M. J. (1984) 'Resource Limitation and Recruitment Patterns in a Coral Reef Fish assemblage', *Mar. Biol. Ecol*. Available at: https://ac.els-cdn.com/002209818490039X/1-s2.0-002209818490039X-main.pdf?_tid=db081856-8f22-4900-a389 d00000dfff14&acdnat=1547114278_822d52165a5aee429a648f79a03316ee (Accessed: 10 January 2019).

Simberloff, D. and Dayan, T. (1991) 'The Guild Concept and the Structure of Ecological Communities', *Annual Review of Ecology and Systematics*. Available at: https://www.jstor.org/stable/2097257 (Accessed: 5 June 2019).

Soares, M.D.O., Rossi, S., Martins, F.A.S., and de Macedo Carneiro, P.B. (2017) 'The forgotten reefs: benthic assemblage coverage on a sandstone reef (Tropical South-western Atlantic)', *Journal of the Marine Biological Association of the United Kingdom*. Cambridge University Press, 97(08), pp. 1585–1592. doi: 10.1017/S0025315416000965.

Stephens, J. S., Hose, J. E. and Love, M. S. (1988) 'Fish Assemblages as Indicators of Environmental Change in Nearshore Environments', in *Marine Organisms as Indicators*. New York, NY: Springer New York, pp. 91–105. doi: 10.1007/978-1-4612-3752-5_5.

Stewart, B. D. and Melbourne, H. (1998) 'Interactions between Piscivorous Coral Reef Fishes and their Prey'. Available at: https://researchonline.jcu.edu.au/27168/1/27168_Stewart_1998_thesis.pdf (Accessed: 14 January 2019).

Thompson, A. and Mapstone, B. (1997) 'Observer effects and training in underwater visual surveys of reef fishes', *Marine Ecology Progress Series*, 154, pp. 53–63. doi: 10.3354/meps154053.