**Temporal effectiveness of biodiversity surrogates in**

**coral reefs in the British Virgin Islands**

Nicole B. Keefner

Biological and Environmental Sciences

Temporal effectiveness of biodiversity surrogates in coral reefs in the British Virgin Islands

Nicole B. Keefner1

1Department of Natural Resources Science, University of Rhode Island, Kingston, RI 02881, USA.

# Abstract

Biodiversity is declining around the world, necessitating rapid identification of species distribution contractions and population declines to identify conservation priorities. Surrogates are increasingly being used to meet this challenge. A good surrogate is expected to be easier to monitor than the target component of biodiversity and meets the assumption that the target-surrogate relationship is constant over space and time. Our objective was to evaluate the spatio-temporal stability of surrogates in coral reef systems around using data from an ongoing 26-year monitoring program in the British Virgin Islands that has quantified the abundance of fish, coral, and sponge species at 8 sites. Of these taxa, corals are the most widely monitored and measures of coral cover are often assumed to be good surrogates for diversity of reef-associated taxa. We thus hypothesize that coral cover and rugosity will be good surrogates for fish, coral, and sponge species richness (the targets). We also investigated how the inclusion of recognizable taxonomic units (RTU’s) compares to species-level studies. We sought correlated relationships between the proposed surrogates and fish, coral, and sponge species richness. Our results provide insight on the use of surrogates in a coral reef ecosystem and on the inclusion of RTU’s in biodiversity studies. The identification of surrogates that maintain stable relationships with target components of biodiversity over time can inform decisions regarding existing data from monitoring studies and the allocation of limited resources for collection of future data.

# Introduction

Biodiversity changes and declines associated with increasing levels of anthropogenic stress disrupt community dynamics and are of great concern because biodiversity contributes to ecosystem function (Emmett Duffy, 2009; Staudinger et al., 2013; Stork, 2010). There are many aspects of biodiversity: landscape, ecosystem, taxonomic, and genetic diversity (Duelli & Obrist, 2003; Noss, 1990). Taxonomic diversity, particularly the diversity of species, is fundamental to understanding evolutionary patterns of distributions, interspecific interactions, and environmental conditions.Species diversity is, consequently, the most commonly measured component of biodiversity in ecological and conservation-related field studies. Species diversity is usually estimated in the field using measures such as species richness, evenness, and diversity indices; richness is the count of species in a given area, evenness a measure of the relative abundance of each species in an area, and diversity indices express a combination of richness and evenness (Hamilton, 2005).

Unfortunately, a complete inventory of species present is unattainable in many ecosystems and, for taxonomic groups that can be inventoried in principle, monitoring strategies that could detect all species in a given habitat are often prohibitively expensive and time-consuming (Kati et al., 2004). In practice, surrogates are often used as simple indicators that provide an estimate of a target component of biodiversity (Magierowski & Johnson, 2006). An effective surrogate takes less time, money, and experience to measure than the target and maintains a consistently strong correlation with the target over time and space (Magierowski & Johnson, 2006).

Ecological dynamics commonly change across spatial scales, thus it is not surprising that most surrogate studies to date have investigated the effectiveness of surrogates across spatial scales. The prevalence of studies considering surrogates across spatial scales may also be due to the widespread use of surrogates to identify priority conservation areas; this task requires an understanding of how the size and dispersion of the areas being conserved will affect the dynamics between the surrogate and target (Margules, Pressey, & Williams, 2002; Padoa-Schioppa, Baietto, Massa, & Bottoni, 2006; Sarkar & Margules, 2002; T. Ward, Vanderklift, Nicholls, & Kenchington, 1999). However, few studies have explicitly investigated surrogate effectiveness across temporal scales, and those that have are typically quite short (e.g., 13 months and 1 year) (Magierowski & Johnson, 2006; Rubal, Veiga, Vieira, & Sousa-Pinto, 2011). One of the few longer studies of ten years, which also included different geographic regions, concluded that percent canopy cover was a poor surrogate for bird richness (Pierson, Mortelliti, Barton, Lane, & Lindenmayer, 2016). Another ten year study identified a group of 35 surrogates that successfully predicted changes in the target assemblage of 98 benthic macroinvertebrate species in a temperate brackish system (Bevilacqua et al., 2018).

Another widespread feature of surrogates for species diversity is a reduction of taxonomic resolution. Monitoring at the species level to estimate biodiversity often requires substantial taxonomic expertise (Hirst, 2008; Sebek et al., 2012). Moreover, some species that can be recognized in the lab using morphological features or genetic markers cannot be distinguished in the field during the monitoring surveys often used by practitioners to estimate species richness. Some biodiversity studies have investigated the use of higher levels of taxonomic organization (such as genera, families, or orders) as surrogates for species diversity to compensate for the difficulties of species-level identification (Fontaine, Devillers, Peres-Neto, & Johnson, 2015; Musco, Mikac, Tataranni, Giangrande, & Terlizzi, 2011; Olsgard & Somerfield, 2000). Taxonomic sufficiency, or the use of higher levels of taxonomic organization when species identification is not possible, is useful for studies in which individuals are not phenotypically distinguishable between taxonomic groups. However, it is not always possible to clearly distinguish between two taxonomic groups, either due to morphological similarities or due to changes in taxonomic classification from splitting. When higher levels of taxonomic organization cannot be employed for these reasons, studies sometimes use recognizable taxonomic units (RTU’s) that are defined by readily identifiable characteristics in the field (Derraik et al., 2002).

Coral reefs are biodiversity hotspots that are globally threatened due to environmental and anthropogenic factors, including ocean acidification, persistent high temperatures, and sedimentation (Hughes et al., 2017; Stubler, Stevens, & Peterson, 2016). As such, many reefs are monitored across both spatial and temporal scales. The most commonly measured features are hard coral cover and structural complexity (rugosity). In fact, the temporal decline of these reef features is widely documented because they are so frequently measured (Alvarez-Filip, Carricart-Ganivet, Horta-Puga, & Iglesias-Prieto, 2013; Habibi, Setiasih, & Sartin, 2007; Stokes, Leichter, & Genovese, 2010). These measures make for good surrogates, as they are simple and affordable to measure, yet exactly what level of biodiversity they are a surrogate for and how effective they are over long temporal scales remains unknown.

Here, I evaluate the effectiveness of hard coral cover and rugosity as surrogates for species diversity for major taxonomic groups on coral reefs over time. Specifically, I use percent live hard coral cover and rugosity as surrogates to predict species richness of corals, fishes and sponges using monitoring data from eight sites around Guana Island in the British Virgin Islands (Forrester et al., 2015). Reef fishes, hard corals (Scleractinia), and sponges are dominant coral reef organisms that establish and maintain biodiversity by filling multiple functional roles in coral reef systems (Angelini, Altieri, Silliman, & Bertness, 2018). I hypothesize that coral cover will be an effective surrogate for coral species richness because declines in coral cover have been associated with declines in coral diversity (Walton, Hayes, & Gilliam, 2018). Similarly, I hypothesize that coral cover will be an effective surrogate for sponge species richness because declines in coral cover have been associated with increases in sponge cover (Ruzicka et al., 2013), most likely due to competitive interactions between sponges and corals. Although coral cover and sponge richness are expected to be inversely related, coral cover would still be a good surrogate if it predicts sponge richness. Coral cover is often positively associated with fish species richness (Jones, McCormick, Srinivasan, & Eagle, 2004; Pratchett, Hoey, Wilson, Messmer, & Graham, 2011), most likely because larger reefs provide more habitat for fishes and because corals provide fish with food (directly in the case of corallivores and indirectly by providing habitat for prey) and protection from predators. Therefore, I hypothesize that coral cover will be an effective surrogate for fish species richness. I hypothesize that rugosity will be an effective surrogate for fish species richness because greater rugosity should provide a wider variety of structures that may be utilized by a greater diversity of fish species (Darling et al., 2017; Graham et al., 2006; Gratwicke & Speight, 2005; Newman et al., 2015) and fish may respond primarily to the structure of the reef rather than its biological features (Wilson et al., 2009; Wilson, Graham, Pratchett, Jones, & Polunin, 2006). Finally, I hypothesize that rugosity will be an effective surrogate for coral species richness because a greater number of coral species should increase the number of coral morphological types and increase rugosity (Alvarez-Filip, Dulvy, Côteé, Watkinson, & Gill, 2011; Newman et al., 2015).

Reef fish richness has been found to be a better surrogate than coral richness for estimating the pooled diversity of corals and fishes when deciding on areas to become marine reserves (Beger, Jones, & Munday, 2003). However, this finding was not investigated over time. Understanding whether these groups can be used as surrogates for other taxonomic groups, would provide valuable information to managers with limited monitoring resources. I will test the hypothesis that reef fish richness will be a good surrogate for the richness of corals and sponges over time. Sites with the highest reef fish richness are not necessarily the same as those with the highest coral richness (Beger et al., 2003).

# Methods

## Field study design

There were eight study sites around Guana Island in the British Virgin Islands (Fig. 1). All sites were similar in covering 0.6-1.0 hectares of fringing reef adjacent to the island at a depth of 10 m. Sites varied in exposure to prevailing weather; sites on the windward north side of the island are more exposed than those on the southern leeward side. Each site was surveyed annually from 1992-2016, except that sponges were not counted in 1992, 1996-1999, 2004, 1993 at Crab Cove, or in 2014 at Pelican Ghut. All surveys were conducted between June and August. Each year, fish densities, coral cover, and sponge abundances were measured using 3-12 transects (mean = 4.3) per site. Transects were 20-30.4 m long (mean = 29.95), and placed at selected locations within each site using a haphazard sampling approach.

## Survey methods

For each transect at each site, corals, sponges, and fishes were sampled once per year using well-established methods (Fig. 2). Fishes were counted within a belt transect 30 m long x 1.5 m wide, and a T-shaped bar was used to determine the transect width as the diver swam along the transect line. Fish counts were restricted to species that are amenable to visual survey, that is, day-active species that are relatively site-attached and reliably visible to divers. Nocturnal species, highly mobile groups such as mackerels (Scombridae) and jacks (Carangidae) that are transient visitors to the sites, and small cryptic groups like gobies (Gobiidae) and blennies (Blennioidei) that often hide in crevices were not surveyed. Newly recruited juvenile fishes (< 1 month on the reef) were also excluded because their abundance is strongly affected by lunar cycles, which complicates the detection of long-term trends. Because fish were the only mobile organisms of the three taxonomic groups included in this study, the fish survey was conducted first for each transect in order to reduce the bias caused by “spooking” the fish (Emslie, Cheal, MacNeil, Miller, & Sweatman, 2018). The diver responsible for identifying corals used the linear point-intercept method and recorded the substrate or coral group every 0.25 m along the 30-m transect. There were 27 recognizable taxonomic units (RTU’s) of hard corals (Forrester et al., 2015). These point observations were later converted to surface area estimates of percent cover (Ohlhorst, Liddell, Taylor, & Taylor, 1988). Sponges were surveyed using the line intercept method in which any sponge that intercepted the transect was recorded. There were 58 RTU’s of sponges (Forrester et al., 2015).

Differences between observers can influence coral reef survey data, but are unlikely to influence the outcome of this study. Fish and sponge data were collected by a single respective expert observer. Coral data were collected by three observers, but new observers’ species identifications and counts were intercalibrated with those of another observer during a training period of at least 15 dives before their data were incorporated into the study.

## Different survey techniques

If we had a line and sampled enough points along the line (i.e. as the number of points approaches infinity) then the linear point-intercept and the line intercept methods would yield the same results for abundance if we knew which points corresponded to which individuals. As of right now, the line intercept method yields counts of individuals (closer to the truth for abundance) and the linear point intercept method yields points covered by a given species which may be converted to percent cover using methods developed for vascular plants (closer to the truth for cover).

## Measures of diversity

Richness, diversity indices, and evenness (rank-abundance) will all be used as measures of biodiversity. Species richness is the number of species in a given area. Evenness can give us information about dominance-related patterns. Diversity indices are one way to express dominance/evenness and richness at the same time.

## Sampling effort

Species accumulation curves have demonstrated that richness may increase as sampling effort increases until an asymptote is reached that represents true site richness (i.e. the more you look, the more you’ll find). Our study aims to investigate how sampling effort may affect estimates of richness (RTU richness).

Because the data is recorded for each transect for each site in a given year, it must be consolidated to have one record per site per year (sampling unit). The minimum sampling effort is three transects. In cases when there are data for more than three transects at a site in a given year, a species accumulation curve will be simulated and if the difference in number of transects makes a difference in species accumulation, 3 transects will be selected at random (may go back and randomly select 3 different transects to see if results would change).

Two methods were used to consolidate counts within a given sampling unit: (1) sum counts over all transects and divide by the number of transects to get the count per transect and (2) sum counts within each transect and divide each sum by the length of the transect to get count per meter, then sum the counts per meter for all transects and divide by the number of transects to get the count per meter per transect (Equations 1 and 2)

1) 2)

Dividing by the number of transects assumes a linear relationship between effort and richness. Equation 2 accounts for differences in transect length.

## Recognizable taxonomic units

Fish, corals and sponges were identified to the most specific taxonomic group possible in the field. All fish were identified to species, while corals and sponges were identified as multi-species RTU’s (D. Ward & Stanley, 2004) rather than species for the following reasons: (1) taxonomists reassigned taxa thought to be different species to the same species after the study began, (2) taxonomists divided a single species into multiple species after the study began, and (3) several species are visually indistinguishable in the field. In all cases, the lowest resolution RTU was used. For example, in 1994 the coral *Montastraea annularis* was recognized to be three separate species (*M. annularis*, *M. faveolata*, and *M. franksi*) (Weil & Knowlton, 1989). Although the species can now be distinguished visually, and were counted separately after 1994, the aggregate was used because the study began in 1992 before the distinction was discovered.

Identification concerns are:

1)\*\*\*Changing taxonomy (e.g. lumping, splitting) Our study aims to investigate how changes in taxonomic groupings may affect estimates of richness

2) Coarseness of taxonomic level (e.g. species, family), which has often been the focus of taxonomic sufficiency studies

3) \*\*\*Ability to distinguish morphologically identical species that may not be taxonomically related (i.e. recognizable taxonomic units/RTUs) Our study aims to investigate how RTUs may affect estimates of richness

It is especially important to consider these potential issues for long-term studies because methods to distinguish species in the field may improve as our taxonomic understanding changes

\*\*\*look up similarities and differences between taxonomic levels studies comparing biological traist and how if you’re related, you’re probably more similar; aka phylogenetic constraints; how do they control for phylogeny?

We also have uneven taxonomic resolution. We have observed richness which, for corals and fishes, might be able to be reconciled to taxonomic richness, which could, in turn, be used to determine species richness. This observed richness 🡪taxonomic richness and taxonomic richness 🡪 species richness jump assumptions can be tested. For example, if site 1 has 10 RTUs and site 2 has 100 RTUs, does site 2 have 100 times more species than site 1? Or, can we collapse the taxonomic resolution to lowest common taxonomic id and retain the same richness relationships (is this even conceptually useful?)? This would require a simulation/extrapolation of RTUs to species. I could simulate this with fish, but I would need to mimic the pattern of taxonomic relatedness seen in sponges.

-Relationship between species richness and RTU richness: If a site has 10 RTUs, it could have 10 species OR, if 5 of these 10 have 2 species, then 10 RTUs might also be 15 species…basically we can say in this example that 10 RTUs can have 10-15 species

-simulate different outcomes with “observed” vs “truth” by lumping into RTUs OR we know RTUs and potential “truth” so first assume min and then max species richness to create bounds; want to determine if RTU richness is at least proportional to species richness BUT can we provide more? Maybe robust distributions (randomly change data uniformly between 2 and 10 to get estimates; r^2 from 0.5-1 good, but may range from 0-1); what might lead you to predict that this relationship is distorted between groups? Different may be due to close relationships, mimicry, or convergent evolution (see notes in red book)

## Functional groups

Species will also be classified based on their functional role within the ecosystem because the diversity of functional groups has been shown to increase reef resilience (Nyström, 2006). For sponges, the major functional roles consist of erosion, stabilization (accretion), bentho-pelagic coupling, and associations with other organisms such as, settlement substrate for algae, habitat for microorganisms, and protecting bivalves from predation (Bell, 2008). Although not understood as well as the others, bentho-pelagic coupling may have significant impacts on the microhabitats available in the reef because some sponges have pumping rates of two times their own volume of water per hour (Bell, 2008). Coral functional roles will be defined by colony shape and morphology (Bellwood, Hughes, Folke, & Nyström, 2004), as well as life history strategy (Bak & Engel, 1979). Because fish influence the community primarily though their role as consumers, they will be classified by trophic group and maximum body size (Halpern & Floeter, 2008).

## Modeling

The relationships between fishes, sponges, and corals were modeled in a linear regression framework. A model with an interactive effect of sponges and corals was included in case fish do not have a preference for using the structural complexity of corals over sponges for shelter.

We will assume the species within an RTU have the same detectability, abundance, and distribution. An RTU may include one species that may be more common than the other included in the RTU, but we assume not.

# Literature Cited

R Core Team (2017). R: A language and environment for statistical computing.

R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Alvarez-Filip, L., Carricart-Ganivet, J. P., Horta-Puga, G., & Iglesias-Prieto, R. (2013). Shifts in coral-assemblage composition do not ensure persistence of reef functionality. *Scientific Reports*, *3*, 1–5. https://doi.org/10.1038/srep03486

Alvarez-Filip, L., Dulvy, N. K., Côteé, I. M., Watkinson, A. R., & Gill, J. A. (2011). Coral identity underpins architectural complexity on Caribbean reefs. *Ecological Applications*, *21*(6), 2223–2231. https://doi.org/10.1890/10-1563.1

Angelini, C., Altieri, A. H., Silliman, B. R., & Bertness, M. D. (2018). Interactions among Foundation Species and Their Consequences ­ for Community Organization , Biodiversity , and Conservation, *61*(10). https://doi.org/10.1525/bio.2011.61.10.8

Bak, R. P. M., & Engel, M. S. (1979). Distribution, abundance and survival of juvenile hermatypic corals (Scleractina) and the importance of life history strategies in the parent coral community. *Marine Biology*, *54*, 341–352.

Beger, M., Jones, G., & Munday, P. (2003). Conservation of coral reef biodiversity: a comparison of reserve selection procedures for corals and fishes. *Biol Cons*, *111*.

Bell, J. J. (2008). The functional roles of marine sponges. *Estuarine, Coastal and Shelf Science*, *79*, 341–353. https://doi.org/10.1016/j.ecss.2008.05.002

Bellwood, D. R., Hughes, T. P., Folke, C., & Nyström, M. (2004). Confronting the coral reef crisis. *Nature*, *429*, 827–833. https://doi.org/https://doi.org/10.1038/nature21707

Darling, E. S., Graham, N. A. J., Januchowski-Hartley, F. A., Nash, K. L., Pratchett, M. S., & Wilson, S. K. (2017). Relationships between structural complexity, coral traits, and reef fish assemblages. *Coral Reefs*, *36*, 561–575. https://doi.org/10.1007/s00338-017-1539-z

Derraik, J. G. B., Closs, G. P., Dickinson, K. J. M., Sirvid, P., Barratt, B. I. P., & Patrick, B. H. (2002). Arthropod Morphospecies versus Taxonomic Species:a Case Study with Araneae, Coleoptera,and Lepidoptera. *Conservation Biology*, *16*(4), 1015–1023. https://doi.org/10.1046/j.1523-1739.2002.00358.x

Duelli, P., & Obrist, M. K. (2003). Biodiversity indicators: The choice of values and measures. *Agriculture, Ecosystems and Environment*, *98*(1–3), 87–98. https://doi.org/10.1016/S0167-8809(03)00072-0

Emmett Duffy, J. (2009). Why biodiversity is important to the functioning of real-world ecosystems. *Frontiers in Ecology and the Environment*, *7*(8), 437–444. https://doi.org/10.1890/070195

Emslie, M. J., Cheal, A. J., MacNeil, M. A., Miller, I. R., & Sweatman, H. P. A. (2018). Reef fish communities are spooked by scuba surveys and may take hours to recover. *PeerJ*, *6*, e4886. https://doi.org/10.7717/peerj.4886

Fontaine, A., Devillers, R., Peres-Neto, P. R., & Johnson, L. E. (2015). Delineating marine ecological units: A novel approach for deciding which taxonomic group to use and which taxonomic resolution to choose. *Diversity and Distributions*. https://doi.org/10.1111/ddi.12361

Forrester, G., Baily, P., Conetta, D., Forrester, L., Kintzing, E., & Jarecki, L. (2015). Comparing monitoring data collected by volunteers and professionals shows that citizen scientists can detect long-term change on coral reefs. *Journal for Nature Conservation*, *24*, 1–9. https://doi.org/10.1016/j.jnc.2015.01.002

Graham, N. A. J., Wilson, S. K., Jennings, S., Polunin, N. V. C., Bijoux, J. P., & Robinson, J. (2006). Dynamic fragility of oceanic coral reef ecosystems, *103*(22).

Gratwicke, B., & Speight, M. (2005). The relationship between fish species richness , abundance and habitat complexity in a range of shallow tropical marine habitats. *Journal of Fish Biology*, *66*, 650–667. https://doi.org/10.1111/j.1095-8649.2005.00629.x

Habibi, A., Setiasih, N., & Sartin, J. (2007). A decade of reef check monitoring: Indonesian coral reefs, condition and trends.

Halpern, B. S., & Floeter, S. R. (2008). Functional diversity responses to changing species richness in reef fish communities. *Marine Ecology Progress Series*. https://doi.org/10.3354/meps07553

Hamilton, A. J. (2005). Species diversity or biodiversity? *Journal of Environmental Management*. https://doi.org/10.1016/j.jenvman.2004.11.012

Hirst, A. (2008). Surrogate measures for assessing cryptic faunal biodiversity on macroalgal-dominated subtidal reefs. *Biol Cons*, *141*.

Hughes, T. P., Kerry, J. T., Álvarez-Noriega, M., Álvarez-Romero, J. G., Anderson, K. D., Baird, A. H., … Wilson, S. K. (2017). Global warming and recurrent mass bleaching of corals. *Nature*, *543*(7645), 373–377. https://doi.org/10.1038/nature21707

Jones, G. P., McCormick, M. I., Srinivasan, M., & Eagle, J. V. (2004). Coral decline threatens fish biodiversity in marine reserves. *Proceedings of the National Academy of Sciences*, *101*(21), 8251–8253. https://doi.org/10.1073/pnas.0401277101

Kati, V., Devillers, P., Dufrˆene, M., Dufrˆene, D., Legakis, A., Vokou, D., & Lebrun, P. (2004). *Testing the Value of Six Taxonomic Groups as Biodiversity Indicators at a Local Scale*. *Conservation Biology* (Vol. 18).

Magierowski, R. H., & Johnson, C. R. (2006). *Robustness of surrogates of Biodiversity in Marine Benthic Communities*. *Ecological Applications* (Vol. 16).

Margules, C., Pressey, R., & Williams, P. (2002). Representing biodiversity: data and procedures for identifying priority areas for conservation. *J Biosci*, *27*.

Musco, L., Mikac, B., Tataranni, M., Giangrande, A., & Terlizzi, A. (2011). The use of coarser taxonomy in the detection of long-term changes in polychaete assemblages. *Marine Environmental Research*. https://doi.org/10.1016/j.marenvres.2010.12.004

Newman, S. P., Meesters, E. H., Dryden, C. S., Williams, S. M., Sanchez, C., Mumby, P. J., & Polunin, N. V. C. (2015). Reef flattening effects on total richness and species responses in the Caribbean. *Journal of Animal Ecology*, *84*, 1678–1689. https://doi.org/10.1111/1365-2656.12429

Noss, R. F. (1990). Indicators for monitoring biodiversity: A hierarchical approach. *Conservation Biology*, *4*(4), 355–364.

Nyström, M. (2006). Redundancy and response diversity of functional groups: Implications for the resilience of coral reefs. *AMBIO: A Journal of the Human Environment*, *35*(1), 30–35. https://doi.org/10.1579/0044-7447-35.1.30

Ohlhorst, S. L., Liddell, W. D., Taylor, R. J., & Taylor, J. M. (1988). EVALUATION OF REEF CENSUS TECHNIQUES. *Proceedings of the 6th International Coral Reef Symposium, Australia*, *2*, 319–324.

Olsgard, F., & Somerfield, P. (2000). Surrogates in marine benthic investigations: Which taxonomic unit to target? *J Aquat Ecosyst Stress Recovery*, *7*.

Padoa-Schioppa, E., Baietto, M., Massa, R., & Bottoni, L. (2006). Bird communities as bioindicators: The focal species concept in agricultural landscapes. *Ecological Indicators*. https://doi.org/10.1016/j.ecolind.2005.08.006

Pratchett, M. S., Hoey, A. S., Wilson, S. K., Messmer, V., & Graham, N. A. J. (2011). Changes in biodiversity and functioning of reef fish assemblages following coral bleaching and coral loss. *Diversity*, *3*(3), 424–452. https://doi.org/10.3390/d3030424

Rubal, M., Veiga, P., Vieira, R., & Sousa-Pinto, I. (2011). Seasonal patterns of tidepool macroalgal assemblages in the North of Portugal. Consistence between species and functional group approaches. *Journal of Sea Research*. https://doi.org/10.1016/j.seares.2011.07.003

Ruzicka, R. R., Colella, M. A., Porter, J. W., Morrison, J. M., Kidney, J. A., Brinkhuis, V., … Colee, J. (2013). Temporal changes in benthic assemblages on Florida Keys reefs 11 years after the 1997/1998 El Niño. *Marine Ecology Progress Series*, *489*, 125–141. https://doi.org/10.3354/meps10427

Sarkar, S., & Margules, C. (2002). Operationalizing biodiversity for conservation planning. *J Biosci*, *27*.

Sebek, P., Barnouin, T., Brin, A., Brustel, H., Dufrêne, M., Gosselin, F., … Bouget, C. (2012). A test for assessment of saproxylic beetle biodiversity using subsets of “monitoring species.” *Ecological Indicators*, *20*, 304–315. https://doi.org/10.1016/j.ecolind.2012.02.033

Staudinger, M. D., Carter, S. L., Cross, M. S., Dubois, N. S., Duffy, J. E., Enquist, C., … Turner, W. (2013). Biodiversity in a changing climate : A synthesis of current and projected trends in the US in a nutshell. *Frontiers in Ecology and the Environment*, *11*(9), 465–473. https://doi.org/10.1890/120272

Stokes, M. D., Leichter, J. J., & Genovese, S. J. (2010). LONG-TERM DECLINES IN CORAL COVER AT BONAIRE, NETHERLANDS ANTILLES. *Atoll Research Bulletin*, (582), 1–21.

Stork, N. E. (2010). Re-assessing current extinction rates. *Biodiversity and Conservation*, *19*(2), 357–371. https://doi.org/10.1007/s10531-009-9761-9

Stubler, A. D., Stevens, A. K., & Peterson, B. J. (2016). Using community-wide recruitment and succession patterns to assess sediment stress on Jamaican coral reefs. *Journal of Experimental Marine Biology and Ecology*, *474*, 29–38. https://doi.org/10.1016/j.jembe.2015.09.018

Walton, C. J., Hayes, N. K., & Gilliam, D. S. (2018). Impacts of a Regional, Multi-Year, Multi-Species Coral Disease Outbreak in Southeast Florida. *Frontiers in Marine Science*, *5*(September), 1–14. https://doi.org/10.3389/fmars.2018.00323

Ward, D., & Stanley, M. (2004). The value of RTUs and parataxonomy versus taxonomic species. *New Zealand Entomologist*, *27*, 3–9. Retrieved from http://www.tandfonline.com/doi/abs/10.1080/00779962.2004.9722118

Ward, T., Vanderklift, M., Nicholls, A., & Kenchington, R. (1999). Selecting marine reserves using habitats and species assemblages as surrogates for biological diversity. *Ecol Appl*, *9*.

Weil, E., & Knowlton, N. (1989). A multi-character analysis of the Caribbean coral Montastraea annularis and its two sibling species M. faveolata and M. franksi. *Smithsonian*, *55*(September).

Wilson, S. K., Dolman, A. M., Cheal, A. J., Emslie, M. J., Pratchett, M. S., & Sweatman, H. P. A. (2009). Maintenance of fish diversity on disturbed coral reefs. *Coral Reefs*, *28*(1), 3–14. https://doi.org/10.1007/s00338-008-0431-2

Wilson, S. K., Graham, N. A. J., Pratchett, M. S., Jones, G. P., & Polunin, N. V. C. (2006). Multiple disturbances and the global degradation of coral reefs: are reef fishes at risk or resilient? *Global Change Biology*, *12*(11), 2220–2234. https://doi.org/10.1111/j.1365-2486.2006.01252.x



Figure 1. A map of Guana Island, British Virgin Islands, showing the eight study sites: (1) Grand Ghut, (2) Pelican Ghut, (3) Bigelow Beach, (4) Monkey Point, (5) White Bay, (6) Iguana Head, (7) Crab Cove, and (8) Long Point.

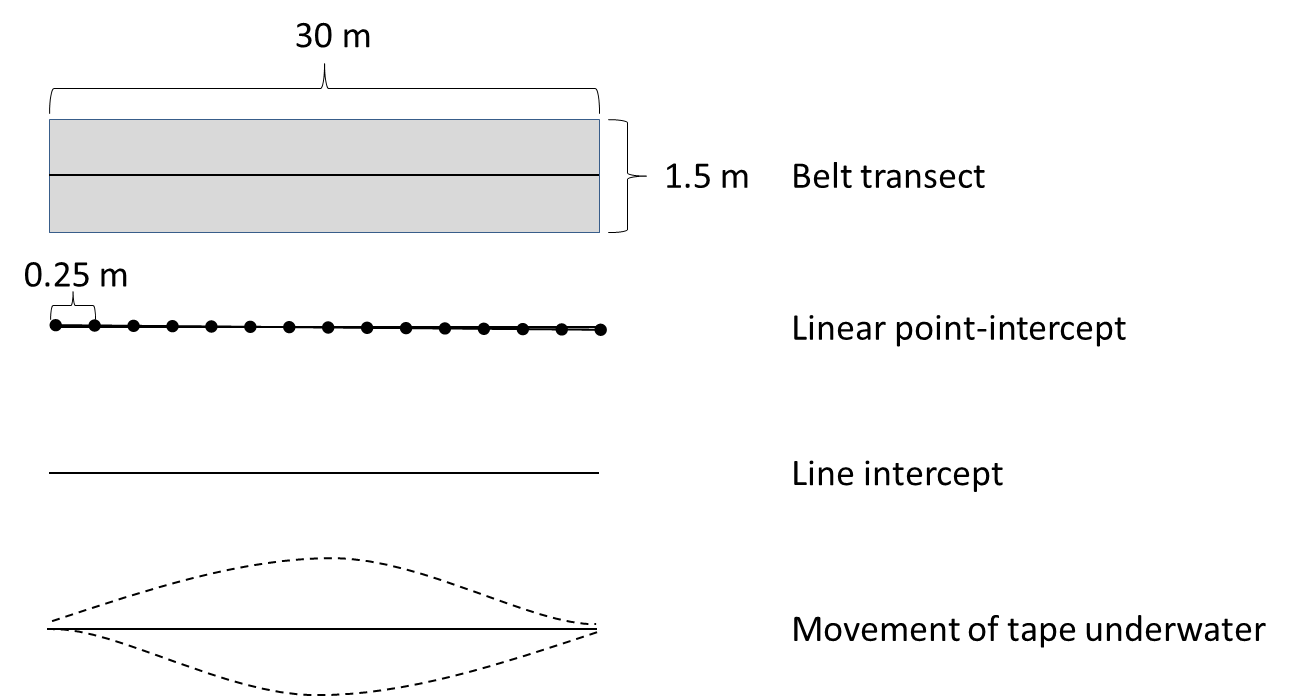


Figure 2. Preliminary depiction of the various transect methods used in this survey.