

Measuring the Effect of Marine Protected Areas on Coral Disease Prevalence Using a  
Meta-analysis Approach

A Thesis submitted in partial fulfillment of the requirements for the degree of Master of  
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by

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## **DEDICATION**

This is dedicated to all the wonderful people in my life who, for the past three years, have given me unwavering support through many late nights with critique and words of encouragement. This is also dedicated to my parents, Bich Van Thi Nguyen and Cuong Van Nguyen, and my brother, Christopher Hieu Nguyen.

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## LIST OF ABBREVIATIONS AND SYMBOLS

Akaike Information Criterion .....	AIC
Akaike Information Criterion, second-level correction .....	$AIC_c$
Bayesian Information Criterion .....	BIC
Clean Water Act.....	CWA
Cochran's measure of heterogeneity .....	$Q_E$
Confidence interval .....	CI
Coral Reef Conservation Program .....	CRCP
Coral Reef Monitoring Project.....	CRMP
Critical value .....	$\alpha$ -value
F-test .....	$F$
Geographic information system.....	GIS
Hawai'i Coral Disease Database.....	HICORDIS
Higgins and Thompson's measure of inconsistency .....	$I^2$
National Oceanic and Atmospheric Administration .....	NOAA
Non-governmental organization .....	NGO
Preferred Reporting Items for Systematic Reviews and Meta-Analyses.....	PRISMA
Probability value .....	$p$ -value
Regression coefficient.....	$\beta$
Residual heterogeneity .....	$Q_M$
Risk difference .....	RD
Sample size (source level) .....	$n$
Sample size of studies (meta-analysis) .....	$k$
Standard error.....	SE
Studentized deleted residuals .....	$t_i$
United States of America .....	US

## **ABSTRACT**

### **MEASURING THE EFFECT OF MARINE PROTECTED AREAS ON CORAL DISEASE PREVALENCE USING A META-ANALYSIS APPROACH**

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George Mason University, 2021

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With corals threatened worldwide from multiple stressors, the evaluation of coral reef management strategies is critical to effectively manage and conserve these ecosystems. One management strategy is a marine protected area (MPA). This thesis endeavored to evaluate whether MPAs were effective in managing coral disease and describes a systematic review to collect data from independently researched sources of coral disease prevalence within and outside of MPAs and the synthesis of these data in meta-analysis models. Risk difference was calculated from prevalence data either as total averages per source, inside and outside MPAs, or by averaging prevalence based on MPA age or protection level. Random-effects, inverse variance weighted meta-analysis models were fit to these respective datasets. Ultimately, only the models with covariance estimates calculated by MPA age or protection level had significant probability values, but power analysis showed this significance to be a Type 1 error. The lack of significance and

power for all models was best explained by highly significant heterogeneity for all models, due to variation at the data-collection level (survey methods and disease identification) at the data-reporting level (incomplete data) across all studies.

Recommendations for resource managers and monitoring organizations include reporting usage or protection level of all MPAs surveyed for use as a factor in analysis, increasing raw data accessibility for other analysts, and reducing heterogeneity through consistency in data collection methods. By addressing heterogeneity in coral disease data, a meta-analysis of coral disease prevalence outside and inside MPAs may be possible, providing valuable insight for coral reef managers into the use of MPAs to mitigate disease as a stressor of declining reefs as outbreaks and disease emergence become more common.

## **CHAPTER ONE**

### **Introduction**

As coral reefs continue to decline due to multiple stressors, most being anthropogenic (Bellwood et al., 2004; Cesar et al., 2003; Hughes et al., 2003), the review of resource management and conservation strategies to protect coral reefs becomes more critical. A common management strategy is to establish a management unit or area encompassing part of, or the entirety, of a coral reef, referred to as a “marine protected area” (MPA). These areas are established with specific goals that can be empirically tested over time to confirm the influence of the MPA on the biological community and/or human resource use of the area (Wilkinson et al., 2003).

MPAs can provide several levels of protection, which vary based on usage restrictions and enforcement. Some do not allow any harvest or recreational usage (“no-take” or “marine reserve”), some allow harvest of specific taxa (“partial-take” or “partial-protection”), while others are designated for recreation and general use (“parks”). In addition, different nations have different designations within their own borders. The most assessed MPAs are no-take reserves, which are effective in fisheries recovery (Sala & Giakoumi, 2018) and favored by stakeholders and managers (Cvitanovic et al., 2013; Fernandes et al., 2005). Although MPAs with fewer restrictions or protection guidelines (an overall lower level of protection) have lower measurements of ecological parameters,

such as fish biomass, than no-take areas (Sala & Giakoumi, 2018), the comparison of ecological benefits of MPAs under different levels of protection is understudied.

The effectiveness of MPAs for conserving biological communities, coral reef structure, and fisheries in general has been measured through several ecological parameters with varying and contradicting results. MPAs had increased fish biomass in Palau (Friedlander et al., 2017), species richness in Europe (Claudet et al., 2008), and fish density globally (Molloy et al., 2009), as compared to non-protected areas. A moderate increase in the percent of living coral tissue per unit area as coral cover (i.e., an important metric of reef-framework stability) was observed in MPAs in the Philippines compared to non-protected areas, with older MPAs having a greater increase in coral cover (Magdaong et al., 2014). Coral cover was also observed to increase in comparison to unprotected areas with high human disturbance (Suchley & Alvarez-Filip, 2018). However, reviews of MPAs in other areas have described the lack of strong benefits of establishing MPAs. For example, studies have shown no positive impact of MPAs on coral cover (Bruno et al., 2019), fish density or species richness in Tanzania (Alonso Aller et al., 2017). In fact, in the Florida Keys, coral cover significantly declined for 15 years after the establishment of an MPA (Toth et al., 2014).

Several factors may influence the efficacy of MPAs, and MPA age (Claudet et al., 2008; Molloy et al., 2009; Selig & Bruno, 2010) and size (Vandeperre et al., 2011) are determinants of success in achieving management goals. In a global analysis of 87 MPAs, Edgar et al. (2014) found that no-take, well-enforced, old (>10 years), large (>100 km<sup>2</sup>), and isolated or deep water MPAs were the most successful, with MPAs with at

least 4 out of 5 of these qualities having an increase in fish density and species richness. In addition to these factors, the ability for an MPA to increase reef fisheries stock (measured in biomass, richness, or assemblage) may be related to the health of the corals of the reef being protected (Aburto-Oropeza et al., 2011; Graham et al., 2008; Noble et al., 2013). Currently, there are few studies measuring MPA effectiveness on diseases of the foundational coral species of reefs.

Coral diseases include a wide range of etiologies and effects on individual corals. They are generally separated into the categories of infectious (e.g., caused by viruses, bacteria, and/or protists), non-infectious diseases (e.g., caused by trauma and/or changes in environmental conditions), and diseases that may be caused by combinations of abiotic and biotic factors (e.g., pollution, microorganisms, and seawater temperature) (Kaczmarek et al., 2011; Peters, 2015; Woodley et al., 2008). Complicating the research of coral disease ecology is that the etiology of many diseases, even infectious diseases, remains unknown despite years of research (Moriarty et al., 2020). As a recent example, the emergence of stony coral tissue loss disease (SCTLD) in the Florida Keys in 2014 has caused rapid mortality across the reef tract (Aeby et al., 2019), with spread to other areas of the Caribbean and Gulf of Mexico also causing devastation of local reefs (Alvarez-Filip et al., 2019). Community composition and total carbon production was permanently changed in a section of Mexican reefs in only 8 months (Estrada-Saldívar et al., 2020). Although rapid-response programs have funded monitoring efforts and disease transmission research, the current etiology of SCTLD remains unknown (Iwanowicz et al., 2020). Related to the difficulty of identifying the causes of coral disease, monitoring

coral disease is challenging due to the visual similarity of several diseases and the lack of identifiable causal factors (Ainsworth et al., 2007; Sutherland et al., 2004; Woodley et al., 2008). The classification of diseases surveyed are inherently inaccurate due to this issue, and the sample of diseased coral captured may not fully represent all diseased corals, as coral microbiomes may enter a state of dysbiosis (a departure from the community structure under stable conditions) long before signs of functional impairment occur (Moriarty et al., 2020; Vega Thurber et al., 2020).

In the context of coral reef decline and conservation, coral diseases are typically endemic issues that are exacerbated by global and abiotic stressors, working synergistically with human impacts to cause decline (Rogers, 2009). Disease outbreaks are currently hard to predict and are therefore difficult to control and prevent (Alvarez-Filip et al., 2019; Miller & Williams, 2007). These events have caused managers and researchers to organize strategic plans for mitigating the effects of coral diseases on reefs, including the production of disease tracking dashboards, data and report sharing, and disease intervention and treatment plans (Florida Department of Environmental Protection, 2021; Galloway et al., 2009; Ocean Research & Education Foundation, Inc. & Atlantic and Gulf Rapid Reef Assessment, 2021). As disease outbreaks and bleaching events increase in frequency worldwide (Eakin et al., 2019), particularly as disease has been correlated with increases in seawater temperature (Aeby et al., 2020; Boyett et al., 2007; Caldwell et al., 2016), research on the causes and impacts of coral diseases is increasingly necessary.



The effect of MPAs on managing disease on coral reefs is not clear, as both positive and negative effects have been observed. Disturbances from human impacts that sometimes occur in and near MPAs, such as recreational use (Harriott et al., 1997) and human development (Pollock et al., 2014), can damage coral and leave them susceptible to disease, increasing occurrence and distribution of disease closer to area of high human impact (Green & Bruckner, 2000). This is similar to the effect measured for coral cover increase, in which the increase in coral cover within MPAs is lower for protected areas with human disturbance (Suchley & Alvarez-Filip, 2018). Although some protections can lower disease risk, such as fishing restrictions on herbivorous species (Caldwell et al., 2020), studies of individual reef systems show that establishing MPAs does not provide adequate disease protection, and that disease prevalence may be insignificantly different or even higher in some MPAs (Coelho & Manfrino, 2007; Lamb & Willis, 2011). This may be due to MPAs increasing host density for coral species, as increased host density of other marine species has been shown in models to increase transmission in parasite-host systems of MPAs (McCallum et al., 2005). However, comparative measurements of disease prevalence inside and outside MPAs have shown that disease levels are lower in MPAs with effective fisheries protections (Lamb et al., 2015; Raymundo, 2009), and protected areas have lower levels of disease than unprotected areas after detrimental environmental effects (i.e., a cyclone) (Lamb et al., 2016). This contention may be explained by associations of disease prevalence with factors that may be affected by protection such as fish community assemblage (Raymundo, 2009), coral colony size (Caldwell et al., 2020), and coral cover (Williams et al., 2010), as well as factors that are

not well-regulated by protection such as season (Haapkylä et al., 2010), bleaching events (Cróquer & Weil, 2009), and reef depth (Couch et al., 2014). These factors can lead to high variability in disease prevalence between areas inside MPAs and outside MPAs.

With disease surveys and studies of individual reefs showing conflicting results as to the success of different management strategies, a meta-analysis model might provide clearer results about the effects of MPAs on coral diseases (Borenstein et al., 2009). Meta-analysis is the pooling of extant data of the effect size of a variable collected through primary research or other methods into a summary statistic (Borenstein et al., 2009; Higgins et al., 2021). For ecological data, meta-analysis has become an increasingly popular tool for measuring conservation interventions and creates more significant results than older synthesis methods (such as literature reviews) (Côté & Stewart, 2013; Fernandez-Duque & Valeggia, 1994). Using a meta-analysis model to compare disease prevalence within and outside of MPAs (measuring the effect of establishing MPAs) can highlight the direction and magnitude of the effect of MPAs as a management tool to mitigate coral disease. Although meta-analysis of coral species dynamics has been performed before (Côté et al., 2005), there have been no meta-analysis studies of coral disease dynamics.

As one of the most common measurements of disease in coral reefs, prevalence may be ideal for comparing disease states within and outside of MPAs. Prevalence for a meta-analysis can be coded as a risk ratio, the diseased proportion of the treated population divided by the diseased proportion of the untreated population, or an odds ratio, the ratio of the proportion of diseased to healthy treated individuals to the

proportion of diseased to healthy untreated individuals (Higgins & Green, 2011).

However, risk and odds ratios must be transformed before pooling and are not easily interpretable by individuals who are not knowledgeable about risk statistics (Borenstein et al., 2009). Risk difference, the difference between prevalence of disease in untreated and treated populations, does not need to be transformed for calculation. Risk difference is also more sensitive to the baseline changes of an effect, and since prevalence can vary widely from endemic or chronic levels to outbreak levels and from disease to disease (Miller & Williams, 2007), measuring the effect size of establishing MPAs on coral disease with risk difference may be a better standard to reduce outliers during analysis. In addition, the data for risk difference are more easily obtained, as only prevalence and standard error are required (Borenstein et al., 2009).

There are several confounding factors with measuring prevalence of coral diseases on reefs that involve measurement methodology, such as difficulty accurately identifying diseases or coral species, as well as other problems common in environmental meta-analysis, such as incomplete datasets and highly variable environmental conditions (Côté et al., 2005). The heterogeneity of studies of MPA efficacy may also be caused by the inherent differences in MPA design and size, lack of paired controls, proximity to other MPAs, and heterogeneity in reef morphology and composition (Claudet et al., 2008; Selig & Bruno, 2010; Vandeperre et al., 2011). The issue of incomplete datasets is more difficult to mitigate, but can be addressed by contacting authors of the primary source (Côté et al., 2013).

This study is a novel investigation of the efficacy of MPAs in mitigating coral disease through meta-analysis of studies conducted on coral disease prevalence inside and outside MPAs. The framework established in this study for the systematic review of coral disease prevalence literature and the comparison of MPA and non-MPA sample site data can be used or improved by other researchers seeking to answer similar questions about MPA efficacy. Additionally, this work will add to the scholarship of MPA effects beyond the typical measurement of effects on fisheries. Risk difference, the summary statistic of the pooled prevalence data, shows both the direction and magnitude of the effect of MPAs on coral disease prevalence. Risk difference in this study is defined as subtracting prevalence within MPAs from prevalence outside MPAs. Each summary statistic created was tested for significance. The null hypothesis tested was that the risk difference between the prevalence inside MPAs and outside MPAs would be equal to zero. The prevalence outside MPAs was predicted to be higher, resulting in a positive risk difference, due to MPA protection generally increasing reef resilience to disturbances from bleaching events (Graham et al., 2008; Wilson et al., 2012), climate change (Roberts et al., 2017), and natural disturbances (i.e., bleaching, disease, predation, and storms) (Mellin et al., 2016), which can decrease the disease prevalence inside MPAs relative to the disease prevalence of areas outside MPAs.

## **Methods**

### **Systematic review**

To accumulate data from primary sources of research while controlling for the effect of variations among research projects, sources were collected through a systematic

review process. The scheme for this systematic review was modified from the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) scheme (Lunny et al., 2017). The body of literature on coral disease prevalence within and outside of MPAs was found in general scientific databases and coral survey-specific repositories with keyword searches. Keywords were specified for use with each search engine/database, as each system has a proprietary algorithm for interpreting Boolean operators, punctuation, plurals, and synonyms. Full keywords per search are listed in Appendix Table 1. Additional sources were collected from hand-searching (i.e., sampling relevant sources through reading citations of another source, or author publications) and from author correspondence. The results from keyword searches were analyzed for relevance, determined by comparison to selection criteria defined before analysis to mitigate selection bias (Table 1). Sources were initially compared to selection criteria for relevance from the title and abstract alone. Sources determined to be relevant were saved and evaluated in the second step, in which the entire article was read for usable data and relevance. Sources with incomplete data were saved and marked, and the listed contact from the source was e-mailed. Relevant sources without complete data and no author reply were excluded from the final dataset (Figure 1).

## **Data extraction**

*Primary source data extraction.* The data collected from each source included coral disease prevalence data within and outside MPAs, citation data and moderator variables. Moderator variables that were considered to have a potential impact on the effect size of each study were recorded along with the effect size and standard error (see

**Table 1. Selection criteria in full**

Inclusion Criteria	Exclusion Criteria
Study measures coral disease prevalence (proportion of diseased corals over total coral in study area)	Study defines marine protected area as park with no usage limitations (“marine protected area” as area with limited usage or established restrictions)
Study measures coral disease prevalence within and outside of marine protected areas	Does not include information on sample methodology or protection level
Document is in English	Document is not in English

below for how to calculate effect size). These variables included country/nation, marine biogeographic province, sampling method (including sampling area size, type, and depth), time of observation (including month and season), management level, and MPA usage. Sources without values on a given moderator variable were recorded as “unknown.”

***Database data extraction.*** Databases containing survey data of coral disease prevalence within and outside of MPAs from coral reef conservation non-governmental organizations (NGOs), state and local governments, and other coral survey agencies were collected from general databases, data.gov and the National Oceanic and Atmospheric Administration (NOAA) OneStop repository of raw data. While these data were not collected with the express purpose of scientific and statistical comparison of MPA efficacy, the measurement of raw data (analogous to individual participant data in medical meta-analysis) allowed the calculation of risk difference and standard error per dataset. Data extracted from these sources included the sample size of diseased corals (by species, disease, location), total sample size/sample size of apparently healthy corals, location, and all available moderator variables.

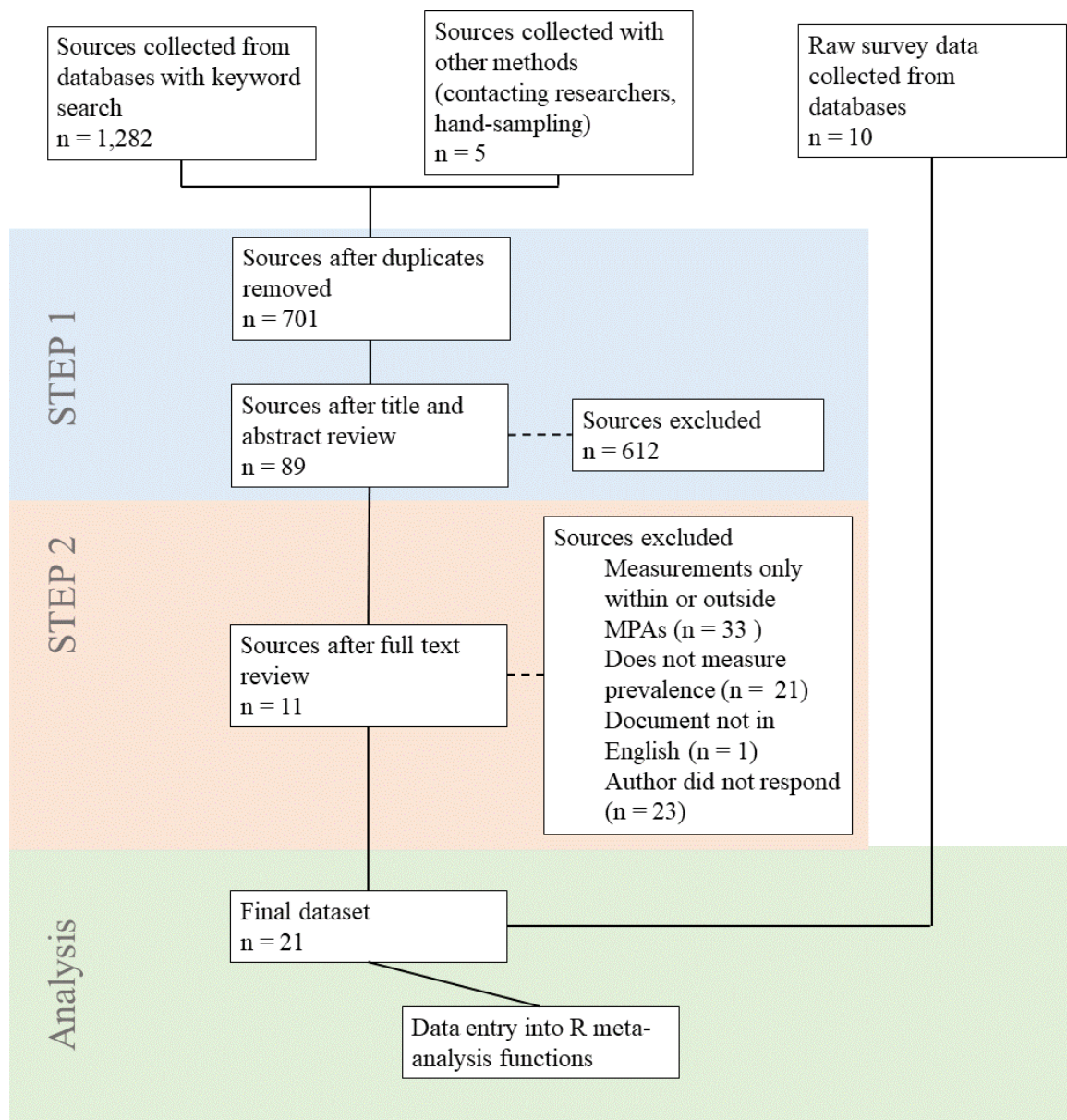


Figure 1. Meta-analysis workflow, adapted from the PRISMA scheme.

**Site MPA status and MPA description.** All available location data were extracted from sources as coordinates in comma-separated value files. Location data were uploaded as a layer in ArcGIS Online, in a map with the NOAA MPA inventories geographic information systems (GIS) layer (NOAA National Ocean Service, Office of National

Marine Sanctuaries, MPA Center, 2020), and MPA establishment year, protection level, and other MPA descriptive data were collected per site of all sources. For sources with locations within MPAs not captured in the MPA inventory (such as those in the Philippines), site data were compared to other documentation on MPAs of the location/nation-state (Appendix Table 3), and protection level was categorized into the “Definitions and Classification System” by the U.S. National Marine Protected Areas Center (National Marine Protected Areas Center, 2020). Sources without location data were not included in the dataset of effect size calculated per MPA age and protection level (Appendix Table 4).

### **Effect size calculation**

*Calculating general effect size.* For sources with raw count data per site and raw dataset sources, disease prevalence for all sites/locations within MPAs and outside MPAs was calculated. The risk difference (RD) was calculated using Equation 1, and the standard error was calculated using Equation 2. For sources with a listed average prevalence for MPA sites and non-MPA sites and no total count data, the risk difference was calculated using Equation 1. The standard error of the risk difference was then calculated with Equation 3 by first calculating the confidence intervals of the risk difference. For Bruckner (2010), prevalence and total coral sample size were given per site. These prevalence data were averaged and grand standard errors for within-MPA sites and outside-MPA sites were calculated. The risk difference was then calculated using Equation 1, and standard error of the risk difference was calculated using Equation



3. Risk differences calculated only considering MPA status per site are referred to as “general prevalence data” for the remainder of this paper.

**Equation 1. Risk difference**

$$RD = prevalence_{out} - prevalence_{in}$$

**Equation 2. Standard error**

$$SE_{RD} = \sqrt{prevalence_{out} * \frac{1 - prevalence_{out}}{n_{out}} + prevalence_{in} * \frac{1 - prevalence_{in}}{n_{in}}}$$

**Equation 3. Standard error (no sample size)**

$$SE_{RD} = \frac{CI_{LB} + CI_{UB}}{3.92}$$

***Calculating effect size separated by MPA age and protection level.*** To calculate the risk differences varying by MPA age and protection level, diseased coral and total coral sample sizes by site were collated by MPA age or protection level (which may include several overlapping MPAs), with all sample sizes from sites outside of MPAs calculated separately. Data from overlapping MPAs were calculated as the oldest MPA group represented in the overlap or the highest level of protection. Risk difference was then calculated with Equation 1, with the individual prevalence data per MPA age or protection level subtracted from the singular prevalence of sites outside MPAs, with standard error calculated with Equation 2. Prevalence was calculated for sources without raw sample sizes by averaging prevalence data for each MPA age or protection level,

with standard error calculated with Equation 3. Sources from the general prevalence dataset without data on MPA protection level or age per study site or average prevalence were excluded from their respective models.

### **Statistical analysis**

**General prevalence model.** All analyses were performed with the R statistical program (RStudio Team, 2020) and the packages “meta,” “dmetar,” and “metaphor.” General average prevalence was pooled with a three-level structure weighted random-effects meta-analysis model, with measurement nested within study. A random-effects model is preferred for meta-analyses that contain mostly observational data (as opposed to the random control data common in clinical trials), and which pool sources from several locations, such as the data in this study (Kulinskaya et al., 2008). Significance testing of the estimated summary effect size was performed through a one-tailed t-test, and the probability ( $p$ -value) of this test had a critical value ( $\alpha$ -value) of 0.05. The assumed null value for significance testing is  $RD = 0$  (no difference in disease prevalence between inside MPA and outside MPA sites). Weight was calculated with inverse-variance. Summary risk difference was calculated with restricted maximum likelihood estimation with the Knapp-Hartung adjustment. The measurement of the quality of fit for a meta-analysis model relies on the interpretation of the effect size estimate, the heterogeneity, and the  $p$ -value of significance testing the effect size estimate. At the core of the critique of meta-analysis is the impertinence of comparing disparate studies with little to no relation to each other (the “apples to oranges” problem) (Borenstein et al., 2009; Higgins et al., 2021). The dissimilarity of the pooled studies is reflected in the

heterogeneity measure Cochran's  $Q_E$ , from which  $I^2$  is derived. In this study, heterogeneity was measured with  $Q_E$  and  $I^2$ . An  $I^2$  above 75% was considered "high" heterogeneity, supported by the chi-squared significance test of  $Q_E$  ( $\alpha = 0.05$ ).

Subgroup analysis of the general prevalence model was performed through meta-regression of the three-level meta-analysis model, retaining the sources with multiple measurements. Significance of the moderator variables in the model was conducted in an omnibus test of an  $F$  distribution of all regression coefficients, with a significant result indicating at least one moderator variable had a significant effect. The risk difference and standard error of each study was plotted in a funnel plot of risk difference on the x-axis and standard error on the y-axis (Borenstein et al., 2009).

*Moderator coding and clustering.* To model the general prevalence data in subgroups with meta-regression, moderators were dummy-coded in binary form (i.e., 0 or 1). The moderator variables chosen for subgroup analysis were source type (primary or raw dataset), region (Tropical Western Atlantic or Indo-West Pacific), season (containing surveys in Autumn or not), survey method (containing belt transects or not), disease community, and species assemblage. These moderators were called "Primary," "Region," "Season," "Method," "Disease," and "Species," respectively. To code disease community and species assemblage as binary variables, both were clustered individually with a hierarchical method and Jaccard similarity (Finch, 2005; Han et al., 2011). The studies were separated by two clusters at the highest node.

*Outlier analysis.* Two methods were used to assess the dataset for potential outliers. The studentized deleted residuals ( $t_i$ ) were calculated for each study, and studies

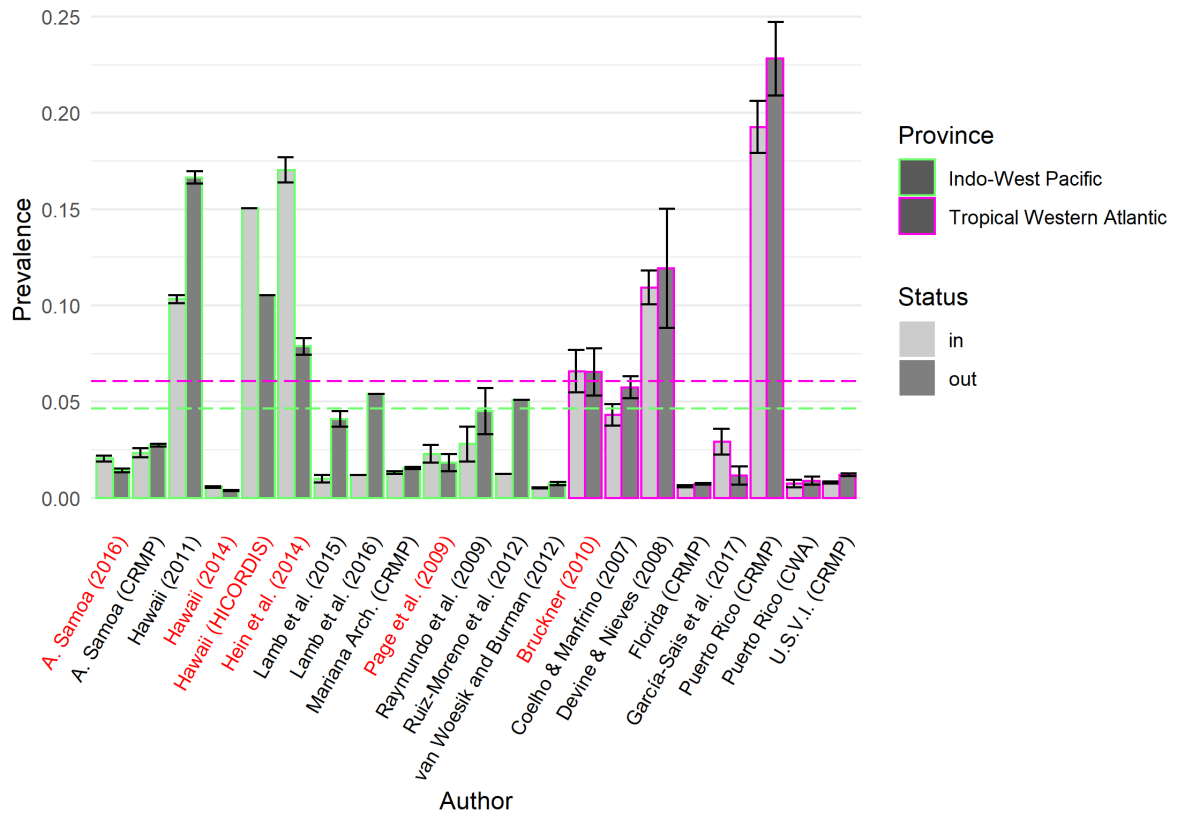
with a residual  $t_i > 1.96$  were considered outliers (Viechtbauer & Cheung, 2010). Outliers were also assessed with confidence intervals per study measurement. Measurements with confidence intervals that did not overlap the confidence interval of the summary risk difference were considered outliers. Outliers were removed from the dataset, and the same three-level model used for the general prevalence data model was re-run to assess changes to the summary effect size and confidence interval (Appendix Table 5).

***Multiple comparison models.*** For both models separated by MPA age or protection level, prevalence data were pooled with a weighted random-effects multivariate meta-analysis model. Weight was calculated with inverse variance. Summary risk difference was calculated with a restricted maximum likelihood estimation with the Knapp-Hartung adjustment. In consideration of MPA age as a continuous variable, summary risk difference was first calculated with a three-level structure meta-analysis model (random-effects, inverse-variance weighted), with two random effects variables: measurement nested within study and MPA age. To account for the covariance introduced by calculating risk difference with only one control per study (average disease prevalence outside MPAs), covariance of the levels of protection or age were modelled with a heteroscedastic compound symmetric covariance structure matrix, in which each level of either MPA protection or age has a difference variance and the same correlation coefficient. As a comparison to the covariance model, the summary risk difference was also calculated with a three-level structure meta-analysis model (random-effects, inverse-variance weighted), with random effects calculated as measurement nested within study and MPA level.

**Power analysis.** Power analysis of these data was performed *post hoc*. The sample sizes of coral were estimated through averaging the available coral sample size data from all sources ( $k = 12$ ) inside MPAs ( $n = 12,783$ ) and outside MPAs ( $n = 19,940$ ). Risk differences were estimated to be values ranging from 0 to 0.05, evenly distributed across 1000 data points to achieve a smooth estimate curve. The heterogeneity component of the variance was estimated as “low” (1.33), “moderate” (1.67), and “high” (2). After the curves were modelled, power estimates using the risk differences of the full general model, MPA age covariance model, and protection level covariance model were calculated with “high” heterogeneity and plotted on the estimate curves.

## **Results**

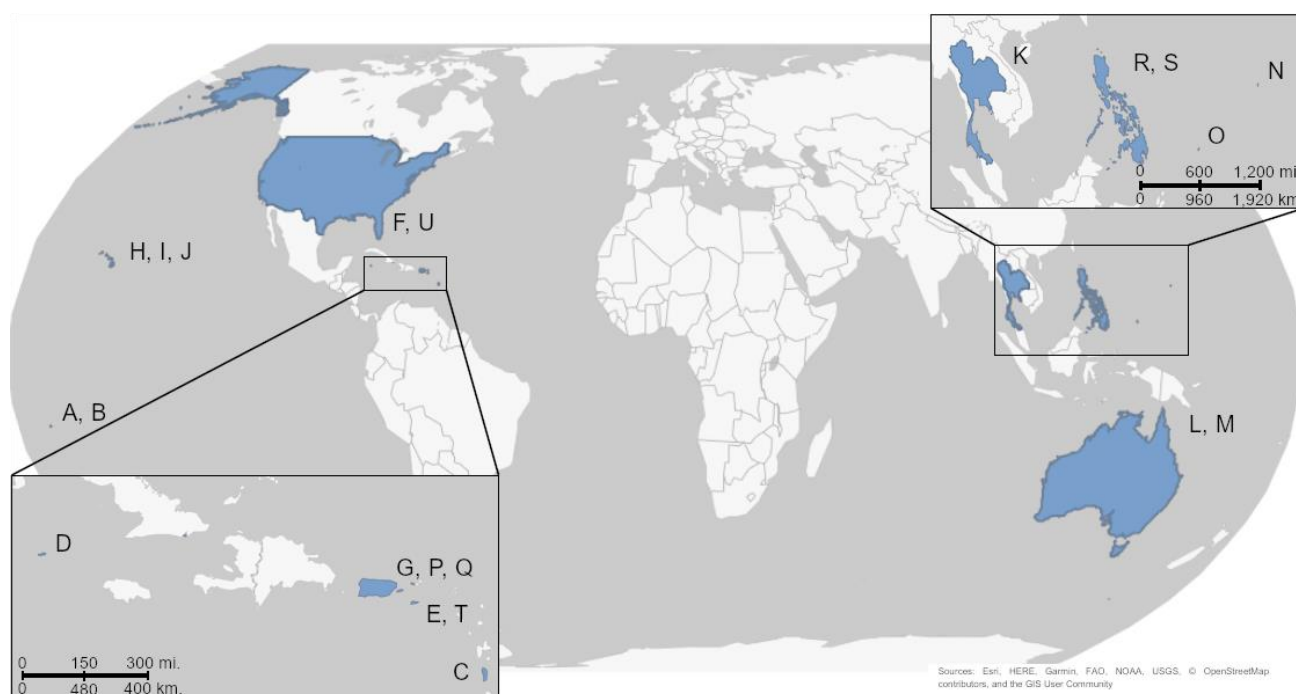
**Data exploration.** The final dataset consisted of 10 raw datasets and 11 primary sources (Appendix Table 2). Of the primary sources, van Woesik & Burman (2012) and Hein et al. (2014) contained raw data provided by the authors. The sources were either from the biogeographic coral reef provinces of the Tropical Western Atlantic ( $n = 9$ ) or Indo-West Pacific ( $n = 12$ ) (Figure 2, 3). The average coral disease prevalences inside and outside MPAs per province were slightly higher outside of MPAs, but not significantly different in either biogeographic coral reef province (Tropical Western Atlantic: Inside = 0.0577, Outside = 0.0638,  $W = 29$ ,  $p$ -value = 0.7984, Indo-West Pacific: Inside = 0.0444, Outside = 0.0483,  $W = 67$ ,  $p$ -value = 0.3897). The total average prevalences of Tropical Western Atlantic and Indo-West Pacific sources were also not significantly different ( $W = 197$ ,  $p$ -value = 0.788). The total average inside MPA



**Figure 2.** Average prevalence ( $\pm$  standard error) per study within (light grey) and outside (dark grey) of MPAs by biogeographic province (Tropical Western Atlantic = pink and Indo-West Pacific = green). The respective average prevalences (combined inside and outside MPAs) for each biogeographic province are represented as horizontal lines. Studies with average prevalence within MPAs higher than average prevalence outside MPAs are highlighted in red. Lamb et al. (2016) and Ruiz-Moreno et al. (2012) averaged across measurements, and standard error not available due to the lack of raw sample size data.

prevalence and outside MPA prevalence, irrespective of province, were also not significantly different ( $W = 197$ ,  $p$ -value = 0.5667).

Diseases ranged greatly in type and assemblage between studies, with five out of the 21 (24%) studies not reporting the type of disease (Table 2). The majority (51%) of pooled sources had MPA ages between 15–35 years (range <1–110 years), with the average MPA age being 28.7 years (Figure 4a). The most common protection level in the pooled dataset was Uniform Multiple Use (39.1%), followed by No-Take (29.0%) (Figure 5a).



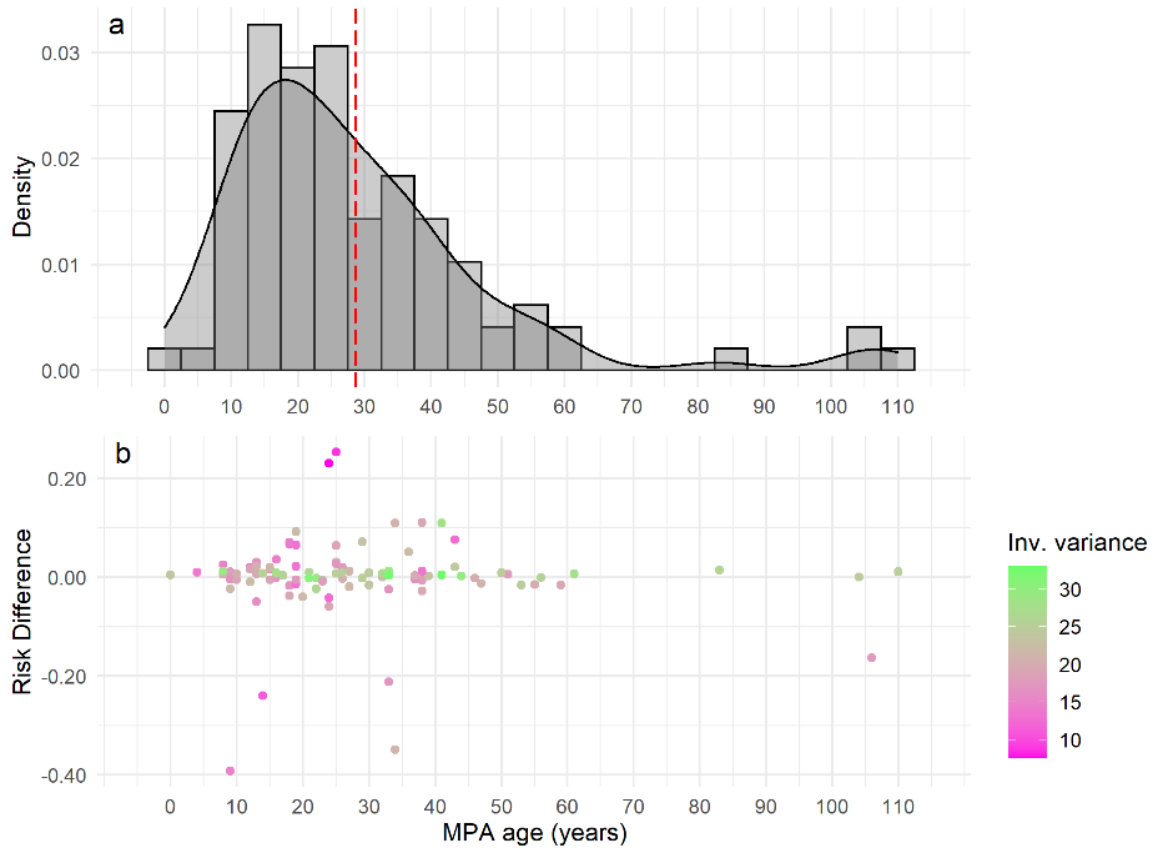
**Figure 3.** World map depicting countries of source sampling sites in blue. Abbreviations for databases are defined in Appendix Table 2. A: American Samoa (2016), B: American Samoa Coral Reef Monitoring Project (CRMP), C: Bruckner (2010), D: Coelho & Manfrino (2007), E: Devine & Nieves (2008), F: Florida (CRMP), G: García-Sais et al. (2017), H: Hawaii (2011), I: Hawaii (2014), J: Hawai'i Coral Disease database (HICORDIS), K: Hein et al. (2014), L: Lamb et al. (2015), M: Lamb et al. (2016), N: Mariana Archipelago (CRMP), O: Page et al. (2009), P: Puerto Rico (CRMP), Q: Puerto Rico Clean Water Act (CWA), R: Raymundo et al. (2009), S: Ruiz-Moreno et al. (2012), T: U.S. Virgin Islands, U: van Woesik & Burman (2012)

**Table 2. Disease assemblage per source**

Source	Disease assemblage
A. Samoa (2016)	algal infection, barnacle infestation, ciliate infection, cyanobacterial infection, discolorations other than bleaching, endolithic fungal infection, growth anomalies, pigmentation response, <i>Porites</i> discolored swelling, trematodiasis, tube worm infestation, white syndrome
A. Samoa (CRMP)	algal infection, barnacle infestation, endolithic fungal infection, growth anomalies, pigmentation response, <i>Porites</i> discolored swelling, sediment damage, sub-acute tissue loss, tube worm infestation, unknown, white syndrome
Bruckner (2010)	black band, Caribbean yellow band, dark spots, white plague
Coelho & Manfrino (2007)	black band disease, dark spots disease, red band disease, white plague disease, yellow blotch disease

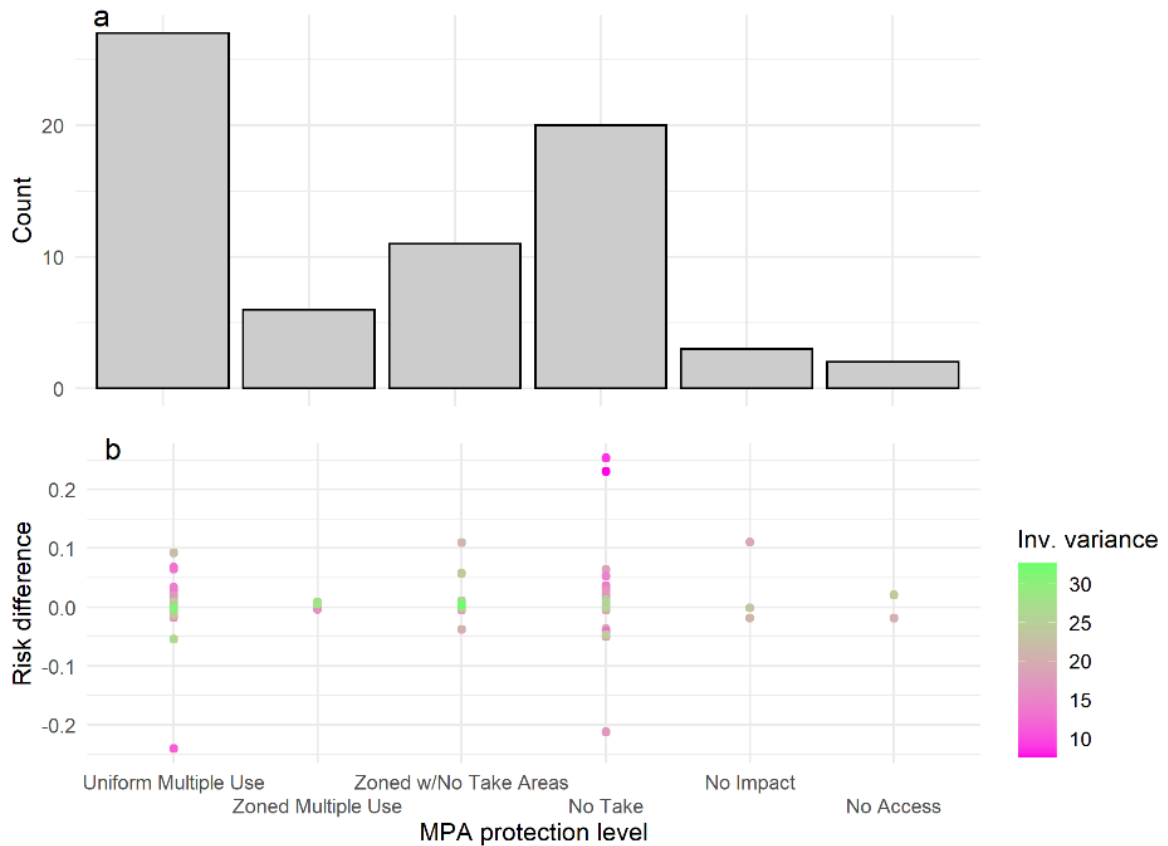
Devine & Nieves (2008)	unknown
Florida (CRMP)	unknown
García-Sais et al. (2017)	black band, Caribbean ciliate infection, dark spots, growth anomalies, pigmentation response, red band, ulcerative white spots, white band, white patch, white plague, white syndromes, yellow band
Hawaii (2011)	algal infection, barnacle infestation, ciliate infection, cyanobacterial infection, discolorations other than bleaching, endolithic fungal infection, growth anomalies, pigmentation response, <i>Porites</i> discolored swelling, sub-acute tissue loss, trematodiasis, unknown, white syndrome
Hawaii (2014)	algal infection, discolorations other than bleaching, discolored tissue thinning, endolithic fungal infection, growth anomalies, other, patchy bleaching, pigmentation response, <i>Porites</i> discolored swelling, sub-acute tissue loss, trematodiasis, tube worm infestation, white syndrome
Hawaii (HICORDIS)	algal infection, algal overgrowth, black band, ciliate infection, cyanobacterial infection, discoloration other than bleaching, endolithic fungal infection, growth anomalies, pigmentation response, recently denuded skeleton, sub-acute tissue loss, swollen patches, trematodiasis, white syndrome
Hein et al. (2014)	atramentous necrosis, black band, broken pieces, brown band, growth anomalies, pigmentation response, sediment damage, skeletal eroding band, sponge overgrowth, unknown, white spot
Lamb et al. (2015)	atramentous necrosis, black band, brown band, growth anomalies, skeletal eroding band, white syndrome
Lamb et al. (2016)	black band, brown band, growth anomalies, skeletal eroding band, white syndrome
Mariana Arch. (CRMP)	algal infection, barnacle infestation, cyanobacterial infection, growth anomalies, pigmentation response, <i>Porites</i> discolored swelling, sub-acute tissue loss, trematodiasis, tube worm infestation, ulcerative white spots
Page et al. (2009)	atramentous necrosis, black band, brown band, cyanobacterial infection, growth anomalies, skeletal eroding band, ulcerative white spots, white syndrome
Puerto Rico (CRMP)	unknown
Puerto Rico (CWA)	unknown
Raymundo et al. (2009)	black band, brown band, growth anomalies, skeletal eroding band, ulcerative white spots, white syndrome
Ruiz-Moreno et al. (2012)	atramentous necrosis, black band, brown band, dark spots, growth anomalies, non-thermal bleach spots, skeletal eroding band, white signs, white syndrome
U.S. Virgin Islands (CRMP)	unknown
van Woesik and Burman (2012)	black band, dark spots, patchy necrosis, red band, unknown, white band, white plague, white spot, yellow band





**Figure 4.** (a) Histogram of MPA ages represented in the dataset with an overlaid density plot. The red vertical line represents the mean MPA age. (b) Scatter plot of risk difference per MPA age. The log values of inverse variance are color-coded, with green representing the highest inverse variance value.

**General prevalence model.** The summary risk difference calculated with the general prevalence model was positive ( $RD = 0.000613$ ) with a confidence interval crossing zero ( $-0.0139, 0.0151$ ) (Table 3). The individual effect sizes in this dataset ranged from  $-0.0916$  to  $0.253$ , with 13 negative risk differences and 28 positive risk differences (Figure 6). This estimate was not significant ( $p = 0.932$ ), and the model had high heterogeneity ( $Q_{E(40)} = 1922.0726, p < 0.0001$ ) (Table 3). Funnel plot analysis for potential publication bias showed possible bias for positive risk differences, indicating a bias for lower prevalences inside MPAs, although the asymmetry is not pronounced (Figure 7).

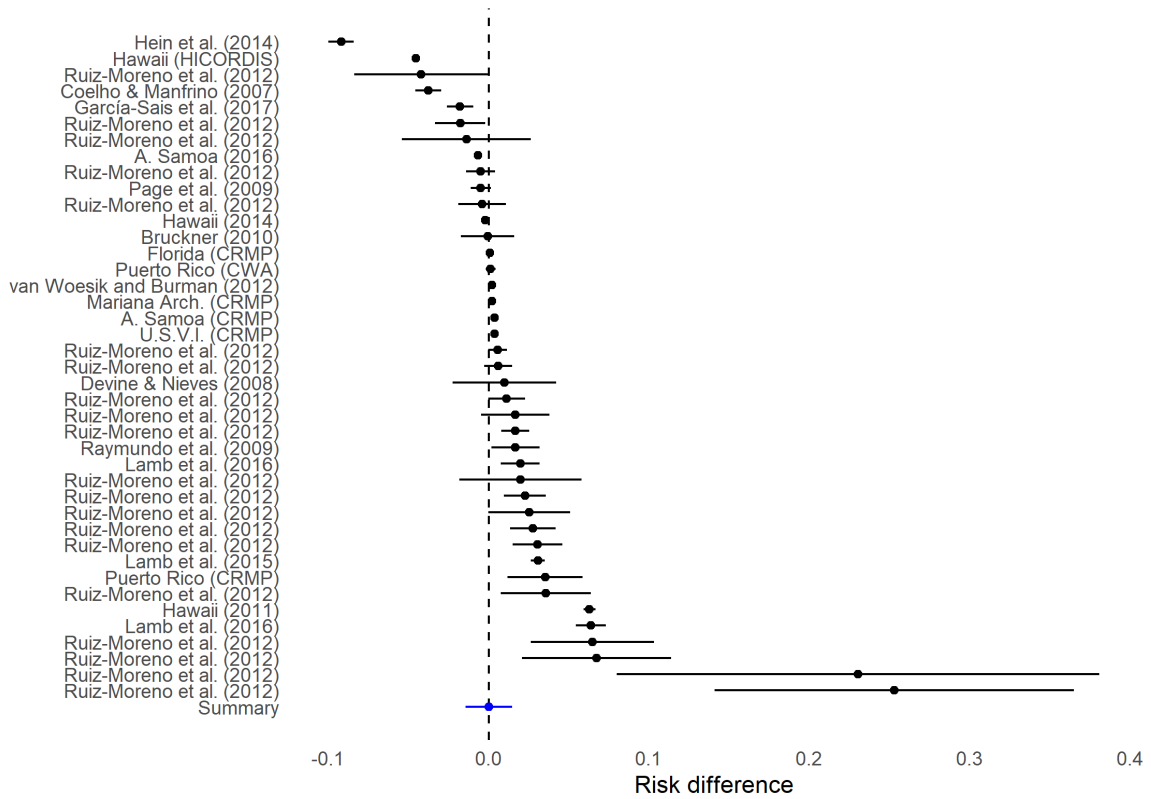


**Figure 5. MPA protection level frequency and risk difference per level (a) Bar chart of the count of all protection levels represented in the MPA protection level dataset. (b) Scatter plot of the risk difference per MPA protection level. The log of inverse variance is color coded, with green representing the highest inverse variance.**

Analyzing the general prevalence dataset with studentized deleted residuals showed five studies to be outliers, representing 25 risk difference measurements (Figure 8, Appendix Table 5). Analyzing the general prevalence dataset with confidence intervals showed 11 measurements to be outliers, with individual measurements selected from studies with multiple measurements (Figure 9, Appendix Table 5). The general model with the outliers determined with studentized deleted residuals removed had a non-significant estimate ( $RD = 0.000711$ ,  $CI = (-0.00712, 0.00854)$ ,  $p = 0.849$ ) and

**Table 3. Model summaries for general disease prevalence, MPA protection level prevalence, and MPA age prevalence.**

	<b>Model</b>	<b>Estimate</b>	<b>Confidence Interval</b>	<b><i>p</i>-value</b>	<b>Cochran's <i>Q</i></b>	<b><i>I</i><sup>2</sup></b>	<b><i>p</i>-value(<i>Q</i>)</b>	<b>AIC</b>	<b>BIC</b>	<b>AIC<sub>c</sub></b>
<b>General</b>	General	0.00061	(-0.0139, 0.0151)	0.932	1922.07	97.919	< 0.0001	-154.86	-149.79	-154.193
	Outlier removed (ti)	0.000711	(-0.00712, 0.00854)	0.849	149.549	89.97	< 0.0001	-75.147	-73.023	-72.965
	Outlier removed (CI)	0.00127	(-0.00122, 0.00375)	0.3054	102.106	71.598	< 0.0001	-169.478	-165.376	-168.518
<b>MPA Protection Level</b>	Covariance	0.00694	(0.00506, 0.00882)	< 0.0001	4694.202	98.551	< 0.0001	-243.033	-225.276	-240.592
	Random variable	-2.36E-05	(-0.00925, 0.00920)	0.9959	4694.202	98.551	< 0.0001	-221.812	-210.714	-220.844
<b>MPA Age</b>	Covariance	0.00694	(0.00577, 0.00811)	< 0.0001	25008.53	99.612	< 0.0001	-151.889	-28.302	-53.889
	Random variable	-0.00181	(-0.0178, 0.0142)	0.823	25008.53	99.612	< 0.0001	-224.511	-214.213	-224.077



**Figure 6.** Forest plot for the general prevalence dataset showing each measurement per source with separate risk difference and corresponding confidence interval, arranged by increasing risk difference. Summary risk difference is shown at the bottom as a blue point, with its corresponding confidence interval.

significantly high heterogeneity ( $Q_{E(15)} = 149.549$ ,  $I^2 = 89.97$ ,  $p < 0.0001$ ). The general model with the outliers determined with confidence intervals removed also had a non-significant estimate (RD = 0.00127, CI = (-0.00122, 0.00375),  $p = 0.3054$ ) and significantly high heterogeneity ( $Q_{E(29)} = 102.106$ , CI = 71.598,  $p < 0.0001$ ) (Table 3).

**Meta-regression.** The summary risk difference was -0.00920. The test for residual heterogeneity (the heterogeneity not explained by the variance caused by moderator variables) was significant ( $Q_{M(34)} = 1418.983$ ,  $p < 0.0001$ ), and the omnibus test for subgroup significance (the heterogeneity caused by at least one of the subgroups being significant) was not significant ( $F_{(7,34)} = 7.2583$ ,  $p = 0.2976$ ). Most subgroups (Primary,

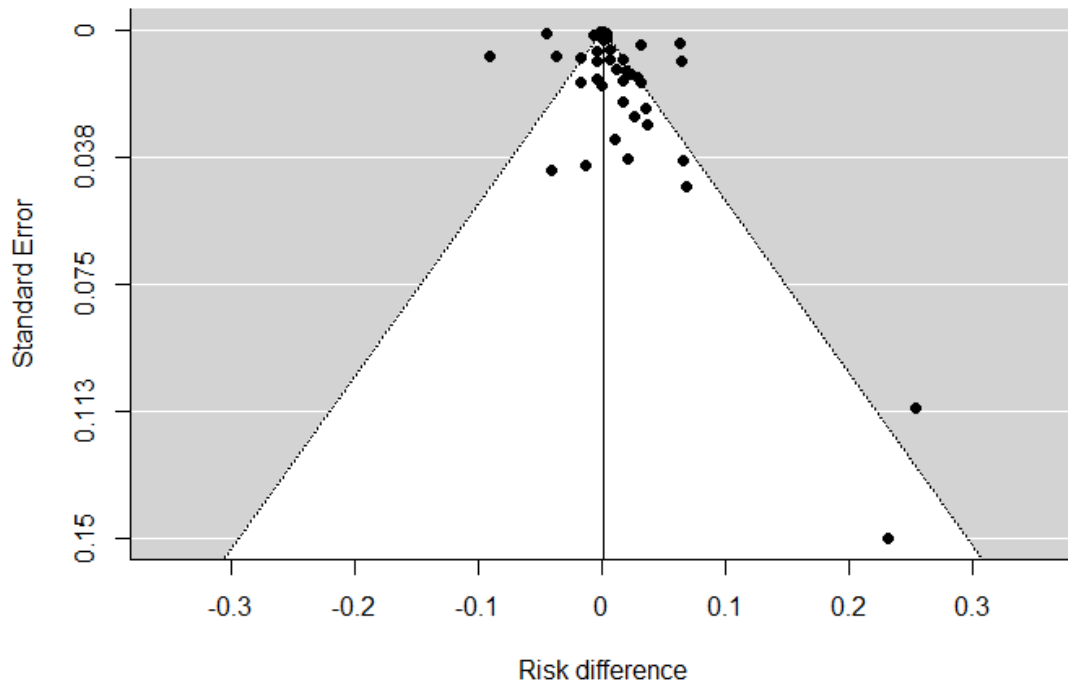
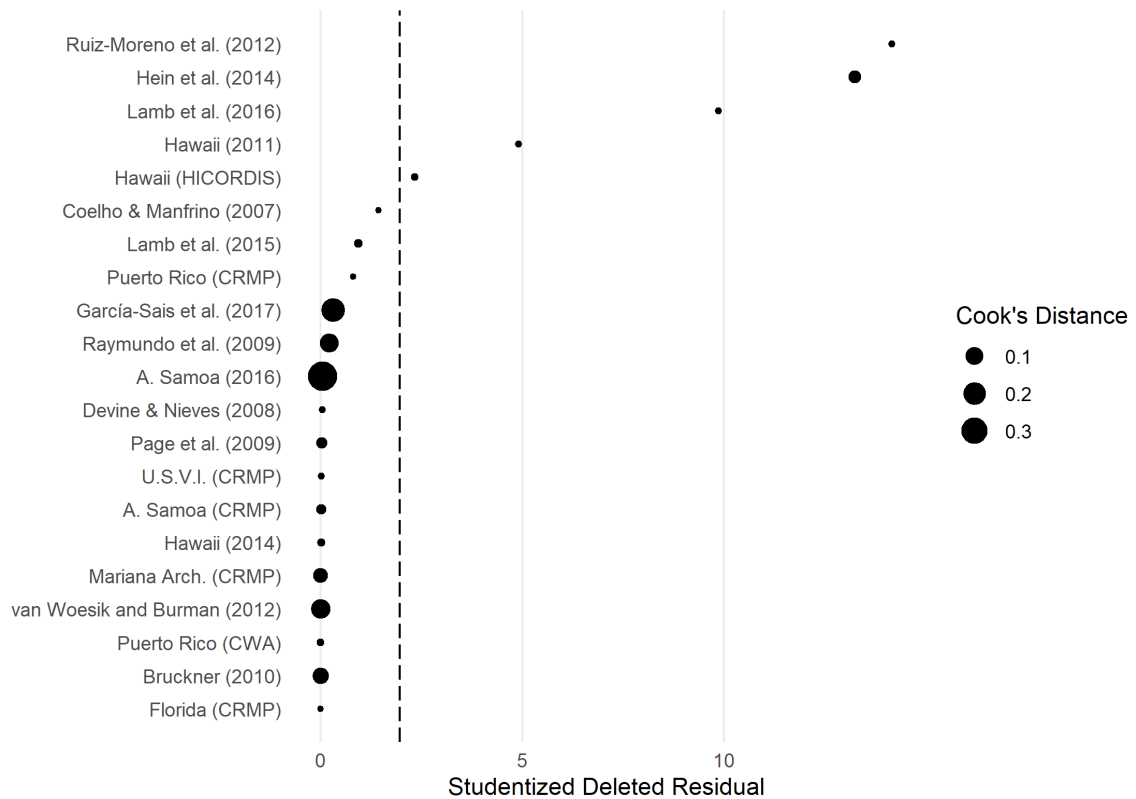


Figure 7. Funnel plot of the general prevalence dataset measurements. The gray area shows a non-normal relationship between the risk difference measurement and standard error.

Region, Method, Disease, and Species) did not have a significant summary risk difference. However, the estimate for the subgroup “Season” was significant ( $p = 0.0340$ ) and negative (RD = -0.0298) (Table 4).

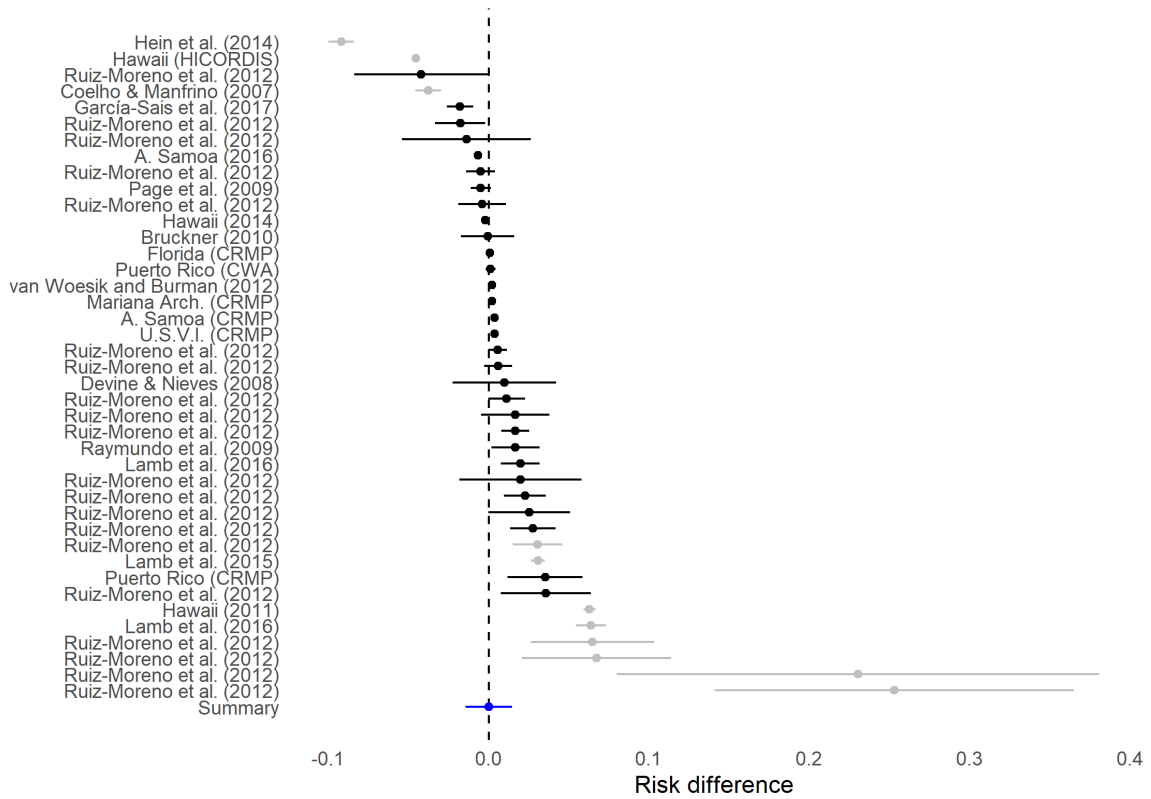
Table 4. Estimates, p-values, and CI of meta-regression model. Significant terms in the model are bolded.

	estimates ( $\beta$ )	Sample size	p-value	CI
intercept ( $\beta_0$ )	0.0273	41	0.3369	-0.0284, 0.0831
Primary	-0.0265	31	0.2099	-0.0679, 0.0149
Region	-0.0274	7	0.3260	-0.082, 0.0272
<b>Season</b>	<b>-0.0298</b>	<b>8</b>	<b>0.0340</b>	<b>-0.0573, -0.0022</b>
Method	-0.0025	33	0.9169	-0.0485, 0.0436
Disease	0.0135	5	0.6228	-0.0402, 0.0671
Species	0.0361	4	0.1655	-0.0149, 0.0871



**Figure 8.** Graph of the studentized deleted residuals per source, arranged in decreasing order of studentized deleted residual, with source as the clustering variable for multiple measurements. The vertical dashed line represents  $t_i > 1.96$ , with values to the left of this line considered outliers. Cook's distance is shown with the size of the points, with larger points having a larger Cook's distance.

***MPA protection level model.*** The summary risk difference calculated from the covariance method was positive ( $RD = 0.00694$ ) with a confidence interval that did not cross zero ( $CI = (0.00506, 0.00882)$ ). The individual risk differences ranged from -0.240 to 0.253, with 25 negative risk differences and 44 positive risk differences. This estimate was significant ( $p < 0.0001$ ) and had significant heterogeneity ( $Q_{E(68)} = 4694.202$ ,  $I^2 = 98.551$ ,  $p < 0.0001$ ) (Table 3). The summary risk difference calculated from the random variable method was negative and small ( $RD = -2.36E-05$ ) with a confidence interval that crossed zero ( $CI = (-0.00925, 0.00920)$ ). This estimate was not significant ( $p = 0.9959$ ).



**Figure 9.** Forest plot of the general prevalence dataset with outlier confidence intervals highlighted, with grey points and confidence intervals indicating outlier status, arranged by increasing risk difference. The summary risk difference is symbolized with a blue point and confidence interval.

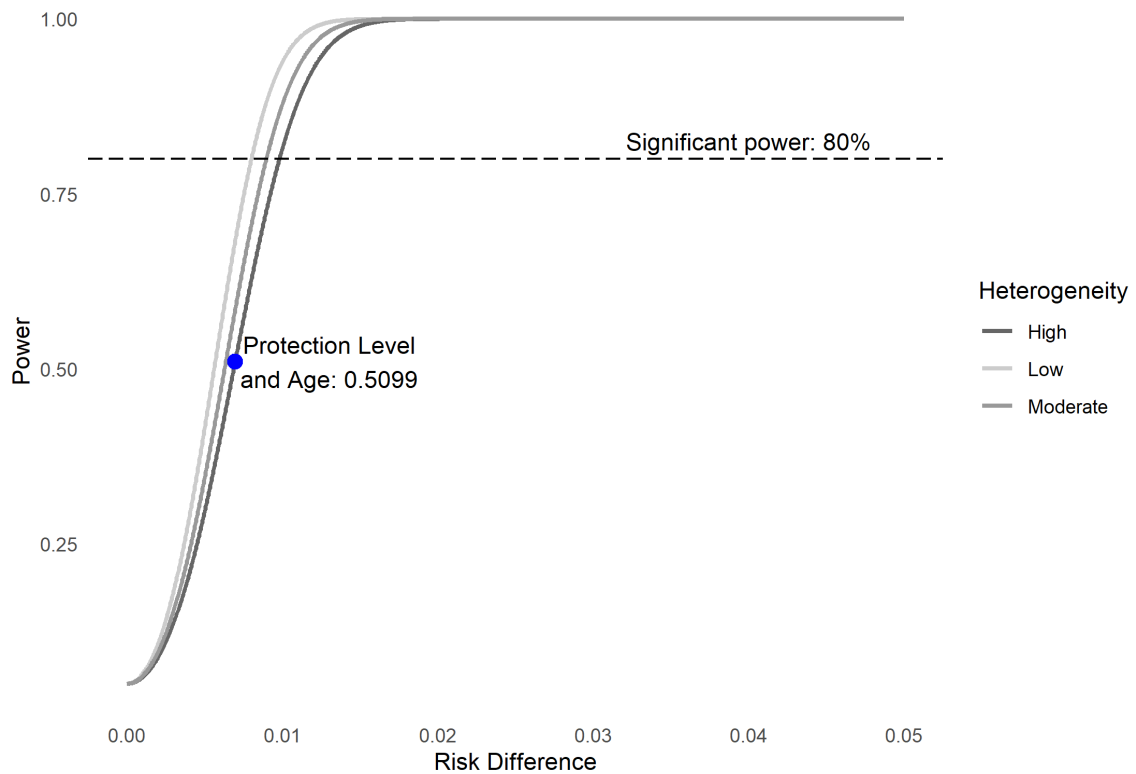
and had high heterogeneity ( $Q_{E(68)} = 4694.202$ ,  $I^2 = 98.551$ ,  $p < 0.0001$ ) (Table 3).

**MPA age model.** The summary risk difference calculated from the covariance method was positive (RD = 0.00694) with a confidence interval that did not cross zero (CI = (0.00577, 0.00811)). The individual risk differences in this model ranged from -0.393 to 0.253, with 39 negative risk differences and 59 positive risk differences. This estimate was significant ( $p < 0.0001$ ) and had significant heterogeneity ( $Q_{E(97)} = 25008.53$ ,  $I^2 = 99.612$ ,  $p < 0.0001$ ) (Table 3). The summary risk difference calculated from the random variable method was negative (RD = -0.00181) with a confidence

interval that crosses zero (-0.0178, 0.0142). This estimate was not significant ( $p = 0.823$ ) and had high heterogeneity ( $Q_{E(97)} = 25008.53$ ,  $I^2 = 99.612$ ,  $p < 0.0001$ ) (Table 3).

**Power analysis.** With the estimated coral sample sizes inside and outside MPAs being 12,783 and 19,440 respectively, power for “low” heterogeneity achieved significance ( $\geq 80\%$ ) at a risk difference of 0.008. Power for “moderate” heterogeneity achieved significance at a risk difference of 0.00896. Power for “high” heterogeneity achieved significance at a risk difference of .0.00981. The “observed power” estimates using the summary risk differences of the general model, MPA protection level model, and MPA age model were 5.337%, 50.53% and 50.53% respectively, and none of the models reached the 80% significance level (Figure 10).





**Figure 10.** Distribution of possible power values for "low", "moderate", and "high" heterogeneity (light grey, medium grey, and dark grey respectively). The “observed” power of both the MPA age covariance model and the MPA protection level covariance model are shown as overlaid blue points.

## **Discussion**

Although meta-analysis is neither fast nor simple to perform, managers may save substantial monitoring costs by considering the use of meta-analysis for describing MPA effects on coral reefs (Côté et al., 2005). Whereas meta-analyses of the effects of coral reef MPAs have been conducted for various effect measures (Magdaong, 2014; Molloy et al., 2009), this research is the first meta-analysis comparing coral disease prevalence inside and outside of MPAs. To achieve this, coral disease prevalence data were collected from primary literature and raw datasets with a global range of sampling sites. A random-effects, inverse-variance model of average risk difference per source (with a three-level

structure to account for multiple measurements per source) did not return a significant summary risk difference ( $RD = 0.000613$ ,  $p\text{-value} = 0.932$ ) and had highly significant heterogeneity (Table 3), indicating that the model could not conclude whether MPAs positively or negatively affected coral disease. Although the positive risk difference may indicate that the establishment of MPAs could keep disease lower inside MPAs versus outside, due to incomplete data as to the prevalence of disease before MPA establishment, this value does not describe whether disease is being decreased in relation to areas outside MPAs compared to prevalence before establishment, or that disease prevalence is maintained at a lower level inside compared to disease prevalence outside. Furthermore, the lack of significance indicates that the true effect size estimated from this dataset may be zero, or even negative. A subgroup analysis of this dataset based on moderator variables returned one significant summary risk difference (Table 4), but with the sample size of this subgroup being under 10, this model is not considered robust. During *post hoc* tests, none of the models achieved significant power. While this may be due to high heterogeneity, the lack of power and significance prompts reevaluation of the data included in this study and the methods used to obtain those data.

***MPAs as effective management strategies.*** The lack of significance for all of the general prevalence data models may be an artifact arising from the lack of agreement of the measured change in parameters due to protection level. The assessment of protected areas as a management strategy for natural resources shows contention and even contradiction between different studies. This disagreement is present globally. In terrestrial protected areas, protection has been associated with positive benefits as

measured through biodiversity (Coetzee et al., 2014; Gray et al., 2016) or abundance of target species (Sáenz-Bolaños et al., 2020) and negative effects such as becoming hotspots for emergent diseases (Lee & Bond, 2016) and failing to prevent species diversity decline (Brown et al., 2019). In marine protected areas, conservation goals such as increasing reef fisheries stock (Aburto-Oropeza et al., 2011; Sala & Giakoumi, 2018) or coral cover (Magdaong, 2014) were met by using MPAs as a management strategy, but other areas have not shown differential increase in fish diversity after establishing MPAs (Machumu, 2013). For managing marine disease dynamics specifically, studies of protected areas have shown positive effects by yielding lower disease levels (Lamb et al., 2015), no measured benefit seen as no significant difference between disease levels (Davies et al., 2020; Page et al., 2009; Wootton et al., 2012), or even deleterious effects, such as increasing transmission (McCallum et al., 2005).

Previous analyses synthesizing global datasets do not show agreement as to the effects of establishing MPAs on coral reefs. Globally, MPAs have been shown to be effective at retaining a given level of coral cover over time (Selig & Bruno, 2010). However, a more recent literature review showed that MPAs did not confer resilience to their respective reefs, as disturbances (e.g., disease outbreaks and extreme weather events) indiscriminately caused significant changes to reef ecological parameters (e.g., coral cover), at sites within and outside of MPAs (Bruno et al., 2019). The differences in the results and conclusions of these studies, which both analyzed MPA efficacy, exemplify the difficulty in making a single, universal statement about the variability in

coral reef ecological parameters based on MPA status alone, possibly due to confounding factors not accounted for in synthesis analysis.

***Meta-analysis for coral disease prevalence.*** No model, including the multiple comparison models, achieved significant power (as calculated with sample sizes estimated with average sample size inside and outside MPAs, respectively) (Figure 10) and only the covariance structure models achieved significant summary risk differences (Table 3). While this may be due to high heterogeneity (discussed below), the lack of power and significance prompts reevaluation of the effect size measure chosen, and suggests coral disease data may be better measured with other effect size measures of binary data which tend to be greater, such as risk ratio or odds ratio (Higgins et al., 2021). For example, a sample with 5 diseased corals of 100 total corals inside MPAs and 7 diseased corals of 100 total corals outside MPAs has a risk difference of  $0.02 \left( \frac{7}{100} - \frac{5}{100} \right)$ , a risk ratio of  $0.714 \left( \frac{5/100}{7/100} \right)$ , and an odds ratio of  $0.699 \left( \frac{5/95}{7/93} \right)$ . As shown in the example, the benefits of risk difference are that directionality can be chosen (in this example, direction was chosen to be consistent with the direction chosen in this study), risk difference is more sensitive to baseline changes (showing greater differentiation between outliers), and risk difference is the most intuitive measure to laymen. Risk ratio and odds ratio must be log-transformed before pooling and must be transformed back before interpretation and are not as easily understandable as risk difference (Borenstein et al., 2009). However, with the same sample size, risk ratio and odds ratio result in higher summary effect size values, improving the possibility of calculating significant power and summary effect sizes even with high heterogeneity. Although this research did not

encompass analysis with other prevalence effect size measures, as a simpler modelling scheme was preferred for this novel analysis, researchers performing further modelling of coral disease prevalence with meta-analysis models should consider using these effect size measurements for initial analysis, and reanalyze and resynthesize the data as risk differences afterward for ease of interpretation and sensitivity analysis (assessing whether significance is maintained) (Higgins et al., 2021).

As a method of investigating the lack of significance of the model estimates, a power analysis was conducted *post hoc*. With the sample size of the data (estimated as the average sample sizes inside MPAs and outside MPAs), the power of this model quickly approached 100% (Figure 10). The “limiting factor” causing power to be below 80% would be the value of the effect size estimate (summary risk difference in this study). Since the estimated disease prevalence on coral reefs is low (~0–5%) at non-outbreak, endemic levels (Ruiz-Moreno et al., 2012), the risk difference between sites within and outside of MPAs can be expected to be 0–5% (positive or negative). This leads to very small risk differences, ranging from -0.00181 to 0.0069 for the general prevalence dataset in this study. Outside of mathematical analysis of the influence of effect size on power, the power of risk difference as an effect size is low (Higgins et al., 2021), and with the variability of the direction of effect size in the datasets (as shown by no dataset having a large majority of risk differences in one direction), power can be expected to be low. The fact that no models achieved significant power in this study may be attributed to these factors, which suggest low feasibility of achieving sufficient power with this dataset and effect size measure. Although a researcher could attempt to reach

power by increasing the sample sizes within and outside MPAs, the use of risk difference as an effect size already decreases power. The high heterogeneity observed in the effect sizes indicates high heterogeneity of risk differences globally, the effects of which may not be adequately overcome simply by increasing sample size. As discussed above, the best method for achieving significant power may be to use a different effect size measure.

Assumptions based on power, in this study the lack of power for any model, must be limited. According to Hoenig & Heisey (2001), the calculation of power *post hoc* may lead to incorrect and improper assumptions when interpreted with the effect size. The lack of significant effect size estimates is not in its entirety explained by the lack of sufficient power, and the fact that power for this study would need a relatively high risk difference (above modelled estimates of endemic disease levels on reefs [Ruiz-Moreno et al., 2012]) is not evidence for the impossibility of risk differences calculated from observed disease prevalence to ever achieve sufficient power. The analysis of the *p*-value and confidence interval of each summary risk difference-model estimate without the context of the *post hoc* power analysis sufficiently describes the possible true effect size, and effect of heterogeneity on calculating the effect size. Importantly, the power analysis in this study provides an explanation of the contradictory model results of the covariance structure models from the multiple comparison group, in which both models had highly significant summary risk difference estimates, but also highly significant heterogeneity (Table 3). The lack of power for these models supports classifying these results as Type I errors, in which the null hypothesis ( $RD = 0$ ) is incorrectly rejected.

A method for managers to perform meta-analysis with higher power (chance of significance) is to limit their sources to one reef system/nation-state. Global datasets from a systematic review may not be large enough to subgroup into individual reefs with a significant sample size ( $k \geq 10$ ), but it may be possible for coral surveys of one nation or reef to create a robust dataset. In this scenario, researchers may reasonably use a fixed-effect model due to the assumption that all sites on a single reef system/nation-state have the same true effect size value, which would lower the requirement for dataset sample size to achieve significance. Even a dataset of  $k = 2$  has higher power in a fixed-effect model than any single study (Borenstein et al., 2009). However, the results of these analyses would be limited to the specific reef system/nation-state only.

The high heterogeneity observed in all models is another reason for the lack of significance observed in summary risk differences. Outlier identification and removal methods (the studentized deleted residual method and the confidence interval method) did not reduce the heterogeneity of the general prevalence dataset for all models except the general prevalence model with outliers determined with confidence intervals removed. Each model having significant heterogeneity, even those with heterogeneity reducing methods, is evidence of the selected studies being too different to pool in one analysis. High heterogeneity is common in meta-analyses of ecology, evolution, and conservation data (Senior et al., 2016) and is directly related to the type of data measured and the difficulty in accounting for all confounding factors (Borenstein et al., 2009).

The observed heterogeneity in this study may be caused by several factors at different levels of this analysis. At the highest level, heterogeneity may have been

introduced at the systematic review, where keywords and selection criteria were intentionally vague (low specificity) to include as many relevant sources as possible. This method is recommended for ecological databases (such as the CoRIS repository) as most are not optimized for meta-analysis (Côté et al., 2013); however, it increases heterogeneity. At another level, heterogeneity may be inherent to these data due to the difference in data collection methods between different research groups and reef managers. In addition, coral disease is difficult to identify in the field (e.g., early biotic disease difficult to detect) (Ainsworth et al., 2007; Moriarty et al., 2020; Sutherland et al., 2004; Woodley et al., 2008) and may lead to high sampling error, which further increases heterogeneity. Heterogeneity may also have been introduced by differences in how standard error was calculated. For example, for some studies, the standard error was calculated by using the confidence intervals calculated by given standard errors (Equation 3) as opposed to those calculated by raw sample size data (Equation 2). Finally, heterogeneity may be inherent to the type of data that were pooled. Although most meta-analyses of medical data are performed on controlled clinical trials (Higgins et al., 2021), the data that were pooled in this analysis are observational, in which each individual sample may be affected by unique factors not considered in data reporting. This makes the data more heterogenous, as well as having less power (Borenstein et al., 2009; Kulinskaya et al., 2008).

A method of analyzing heterogeneity is subgroup analysis. Subgrouping the general prevalence data with the moderator variables chosen (source type, region, season, survey method, disease assemblage, and species community) did not change the



heterogeneity of the data. This may again be explained by the observational nature of the pooled data in that there may be several unknown and confounding variables not captured by the data collection process, and therefore cannot be included in the moderator analysis. A study of MPA assessment suggests incorporating MPA habitat structure and size in addition to the inclusion of MPA protection level, as well as other covariates into measurements of MPAs (Claudet & Guidetti, 2010), which may provide more moderator variables not available for this meta-analysis. Additionally, covariate groups with a sample size less than 10 are not generally considered robust, as subgroups with less than 10 samples will have low power (Borenstein et al., 2009). Season was the only subgroup to have a significant effect size estimate, suggesting that sampling in autumn may cause significant variation in the data. The negative, significant effect size suggests that the prevalence of coral disease inside MPAs may be higher than prevalence outside MPAs during autumn, although extrapolating causality from a meta-regression (particularly in this model, as several of the covariates did not have 10 measurements) is not recommended (Borenstein et al., 2009). Even without assuming causation, this model supports the further investigation of how sampling season might impact disease prevalence measurements. Seasonality of coral disease has been observed in the Great Barrier Reef for brown band syndrome (most prevalent during winter) and ulcerative white spots (most prevalent during summer) (Haapkylä et al., 2010). The difference in the prevalence seasonality of these diseases suggests modelling of coral disease prevalence would have less heterogeneity with prevalence measurements separated by individual disease, supported by evidence of individual coral diseases responding differentially to

different environmental factors in predictive modelling of disease prevalence (Williams et al., 2010).

***Multiple comparison models.*** As discussed above, modelling the effect of establishing MPAs to manage coral disease prevalence with multiple comparison risk difference measures per MPA protection level or age for each source returned significant summary risk differences only for the models with a covariance structure for the risk difference measurements. For these models, the covariance model was predicted to fit each model the best, as to account for the non-independence with a correlation component maintained between all measurements with the same outer variable (source), but with different variance estimates per protection level within the study. The different variance estimates would account for the prediction that each level of protection or each age has a different level of variation, which is supported by the graphs of logarithm of inverse variance values and risk differences per protection level and per age (Figure 4b, Figure 5b). Although pooling risk difference through the calculation of prevalence per MPA protection level or MPA age resulted in a high enough effect size to achieve significance (covariance structure models), all multiple comparison models had highly significant heterogeneity ( $p$ -value  $< 0.0001$ , shown in Table 3), and power analysis of the observed risk difference estimates of the covariance structure models showed insignificant power (Figure 10), suggesting a Type 1 error of incorrectly significant summary risk difference (discussed above).

Due to limitations of the calculation equations for this type of model, age was coerced into a factor with each individual age as a separate, non-related level. The

correlation component calculated in the covariance matrix accounts for the non-independence of the measurements, but does not introduce the correlation of risk differences between MPAs of different ages in the same study. As an MPA gets older, it follows that any benefit from establishing an MPA would increase, as several measurements of coral cover and other coral species parameters have been shown to increase with MPA age (Edgar et al., 2014; Friedlander et al., 2017). Due to the maintained directionality of effect size across increasing MPA age, a completely independent variance estimate per age may overfit the model to the dataset, instead of finding the best fit to describe the true effect size.

For both models, the inclusion of either MPA age or protection level as a random variable term, instead of in a covariance structure, resulted in insignificant risk difference estimates with high heterogeneity (Table 3). These results suggest that accounting for the variance of MPA age and protection levels as a random variable does not sufficiently decrease heterogeneity. It also implies that calculating the variance between different non-independent measurements with a three-level structure only is not precise and is better modelled by a covariance matrix with a maintained correlation component for all levels.

***Model comparison and selection.*** Burnham & Anderson (2004) clarifies that both measure different qualities of model fit and converge on different target models by describing the mathematic concepts underlying both calculations, and the different philosophies of using either for selection. In summation, AIC measures the amount of information lost by choosing one model over the other, and tends to be influenced by the

sample size of the model measured. BIC, although originally described as a measurement of the similarity of one model to a theoretical “true” model of the data, measures the difference from the measured model to a quasi-true model (which is the closest to the target model measured with the same distance measure as AIC). In either case, the lowest value may be used for comparison of models. The lowest AIC selects the model with least information lost with the given model. The lowest BIC selects the model that is closest to the model representing quasi-truth (Burnham & Anderson, 2004). When processing models with low sample size in relation to parameters (which Burnham and Anderson define as sample size  $n$ /parameter size  $K < 40$ ), the corrected AIC,  $AIC_c$ , is more accurate in measuring information lost.

For the general prevalence data model set, which includes the full general model, the general model with outliers determined by studentized deleted residuals removed (study level), and the general model with outliers determined by confidence intervals removed (measurement level), the general model with outliers removed determined by confidence intervals had both the lowest  $AIC_c$  (-168.518) and BIC (-165.376) (Table 3), supporting its selection as the best option to model the general prevalence data. This is also supported by this model having the lowest heterogeneity (indicating it has the lowest between-studies variance). However, all models of this set had significant heterogeneity ( $p < 0.0001$ ) (Table 3), showing that the differences in calculation between the different models do not sufficiently address the underlying heterogeneity of the dataset.

The MPA protection level model set included a multivariate model with covariance of different protection levels modelled as a heteroscedastic compound

symmetric structure matrix, and a three-level multivariate model with protection level modelled as a random variable along with a nested random variable of measurement and study. The covariance model had both the lowest  $AIC_c$  (-240.592) and BIC (-225.276), supporting its selection as the better model of this set. The MPA age model set included two models with the same modelling methods. For this factor, however, the random variable model had the lowest  $AIC_c$  (-224.077) and BIC (-214.213). This difference may be explained by the modelling limitation described above for age as a continuous variable in a covariance structure model. Just as for the general model set, all multiple comparison models had significant heterogeneity ( $p < 0.0001$ ) (Table 3), showing that neither method (covariance or random effect variable) was able to address heterogeneity in the dataset.

### **Conclusions**

The impact of MPAs on any one ecological parameter has been contested for several biological (Alonso Aller et al., 2017; Edgar et al., 2014; Selig & Bruno, 2010; Zvuloni et al., 2009) and statistical reasons (Bruno et al., 2019). Meta-analysis may provide scientists and natural resource managers the ability to synthesize data from multiple studies, generally with higher power than for any individual study (Borenstein et al., 2009; Higgins et al., 2021). For overall disease prevalence of reefs worldwide, the results of this study did not support the hypothesis that there was any difference between disease prevalence inside MPAs and outside MPAs. This may be due to high heterogeneity, low statistical power, or that there truly is no effect of MPAs on coral disease. Although several statistical methods were used to decrease heterogeneity, as recommended in the Cochrane Handbook for Systematic Reviews and Interventions

(Higgins et al., 2021), the best way to decrease heterogeneity and increase the probability of detecting non-zero risk differences (from the models compared) is by collating samples by MPA protection level and estimating the variance of each risk difference per protection level. In addition, the low power for this effect size suggested a Type 1 error, in which the null hypothesis ( $RD = 0$ ) was incorrectly rejected, evidence supported by the significant heterogeneity in this model. Persistent sources of heterogeneity were observed at every level of this analysis (from data collection to pooling) and were difficult to remove, limiting the ability to use meta-analysis models to describe changes in disease metrics.

In consideration of further global scale meta-analysis of coral disease metrics, several recommendations for survey or study reporting can be made to assist with decreasing heterogeneity.

- The results of the covariance model of MPA protection level suggested that the probability of achieving significance with risk difference data increased when protection level was used as a factor with covariance. This suggests the need to report the current MPA protection level for disease surveys. Although the protection level could be categorized through the NOAA MPA inventory, not every MPA was represented in this inventory (Appendix Table 3). By at least carefully reporting usage or protection laws per MPA measured, meta-analysts can use it as a factor.

- Any primary study of coral disease should report as much data as possible, either in text, supplementary info, or in a repository. Data should include raw coral sample sizes, or if possible, individual level data for each coral measured. Reporting of raw sample size can lead to more precise effect sizes of disease (i.e., risk ratio or odds ratio), and gives meta-analysts more flexibility for recalculation of effect sizes.
- Heterogeneity was determined to be one of the driving factors for model insignificance, which as mentioned above, may be due to several factors at the data collection level. By having uniform survey methods, even for primary studies (Durgappa & Hebbale, 2013), more general meta-analysis with global datasets can be conducted with less variability and a higher chance of finding a significance if it really exists.

With these recommendations, individual studies of coral reef disease may have less error and bias, which will lead to less heterogeneity in meta-analysis. The statistical methods mentioned above may also be used to decrease heterogeneity and increase power. Global cooperation and collaboration are needed to implement these changes, as well as increased rigorous monitoring efforts. By sufficiently addressing heterogeneity, meta-analysis may be a tool for coral reef managers to use in assessing the effect of MPAs as a management strategy to mitigate coral disease, giving them invaluable information about their own strategies in the endeavor to slow and reverse coral reef decline.

## APPENDIX

**Appendix Table 1. Full keywords per database**

Database	Keywords Used
Google Scholar, ProQuest Complete	coral + "disease prevalence" + "marine protected area" + usage + MPA
Mason Open Educational Resources Metafinder	"Coral disease prevalence" AND ("marine reserve" OR "marine reserves" OR "marine protected areas" OR MPA)
Science.gov, ScienceDirect, Web of Science Core	("coral disease" OR "coral diseases" OR "black-band disease" OR "white patch syndrome") AND ("marine reserve" OR "marine reserves" OR "marine protected area" OR "marine protected areas" OR MPA)
Washington Research Library Consortium	"coral disease prevalence" AND ("marine reserve*" OR "marine protected area*" OR MPA)
CoRIS (Library Catalog collection)	disease prevalence

**Appendix Table 2. Full citations of all sources included in the general prevalence model.**

Primary source	Raw dataset
Bruckner, A. W. (2010). View of implications of coral harvest and transplantation on reefs in northwestern Dominica. <i>International Journal of Tropical Biology</i> , 58(Supplemental 3). <a href="https://revistas.ucr.ac.cr/index.php/rbt/article/view/32958/32409">https://revistas.ucr.ac.cr/index.php/rbt/article/view/32958/32409</a>	Coral Reef Ecosystem Program, Pacific Islands Fisheries Science Center (2018). Belt transect surveys of coral populations and disease assessments in Hawaii, Maui, and Oahu from 2010-03-08 to 2011-11-08 (NCEI Accession 0168912). (Version 1) [Data set]. NOAA National Centers for Environmental Information. <a href="https://accession.nodc.noaa.gov/0168912">https://accession.nodc.noaa.gov/0168912</a>  Abbreviated as Hawaii (2011)
Coelho, V. R., & Manfrino, C. (2007). Coral community decline at a remote Caribbean island: Marine no-take reserves are not enough. <i>Aquatic Conservation: Marine and Freshwater Ecosystems</i> , 17 (7), 666–685. <a href="https://doi.org/10.1002/aqc.822">https://doi.org/10.1002/aqc.822</a>	Hawai'i Coral Disease database (2004-2015). [Individual colony-level data of various surveys of Hawaiian coral reefs] [Unpublished data set]. NOAA National Centers for Environmental Information. <a href="https://www.ncei.noaa.gov/archive/accession/0128219">https://www.ncei.noaa.gov/archive/accession/0128219</a>



	Abbreviated as Hawaii (HICORDIS)
Devine, B., & Nieves, P. (2008). Developing surface water GPS digital mapping technology to map the spatial distribution of size classes and disease prevalence of elkhorn coral in the nearshore waters of St. Thomas and St. Croix. The Nature Conservancy.	NOAA National Centers for Coastal Ocean Science (2016). National Coral Reef Monitoring Program: Assessment of coral reef benthic communities in the U.S. Virgin Islands. [Data set]. NOAA National Centers for Environmental Information. <a href="https://doi.org/10.7289/v5ww7fqk">https://doi.org/10.7289/v5ww7fqk</a>
	Abbreviated as U.S.V.I (CRMP)
García-Sais, J., Williams, S., Esteves, R., Sabater-Clavel, J., & Carlo, M. (2017). Monitoring of coral reef communities from natural reserves in Puerto Rico: 2017 (NA15NOS4820127; Monitoring of coral reef communities from natural reserves in Puerto Rico, p. 316).	NOAA Pacific Islands Fisheries Science Center Ecosystem Sciences Division (2018a). National Coral Reef Monitoring Program: Stratified random surveys (StRS) of coral demography (adult and juvenile corals) across American Samoa. [Data set]. NOAA National Centers for Environmental Information. <a href="https://doi.org/10.7289/v579431k">https://doi.org/10.7289/v579431k</a>
	Abbreviated as American Samoa (CRMP)
Hein, M. Y., Lamb, J. B., Scott, C., & Willis, B. L. (2015a). Assessing baseline levels of coral health in a newly established marine protected area in a global scuba diving hotspot. <i>Marine Environmental Research</i> , 103, 56–65. <a href="https://doi.org/10.1016/j.marenvres.2014.11.008">https://doi.org/10.1016/j.marenvres.2014.11.008</a>	NOAA Pacific Islands Fisheries Science Center Ecosystem Sciences Division (2018b). National Coral Reef Monitoring Program: Stratified random surveys (StRS) of coral demography (adult and juvenile corals) across the Mariana Archipelago. [Data set]. NOAA National Centers for Environmental Information. <a href="https://doi.org/10.7289/v53n21q5">https://doi.org/10.7289/v53n21q5</a>
	Abbreviated as Mariana Archipelago (CRMP)
Lamb, J. B., Wenger, A. S., Devlin, M. J., Ceccarelli, D. M., Williamson, D. H., & Willis, B. L. (2016). Reserves as tools for alleviating impacts of marine disease. <i>Philosophical Transactions of the Royal Society B: Biological Sciences</i> , 371 (1689). <a href="https://doi.org/10.1098/rstb.2015.0210">https://doi.org/10.1098/rstb.2015.0210</a>	NOAA Southeast Fisheries Science Center, NOAA National Centers for Coastal Ocean Science (2018). National Coral Reef Monitoring Program: Assessment of coral reef benthic communities in the Florida Reef Tract. [Data set]. NOAA National Centers for Environmental Information. <a href="https://doi.org/10.7289/v5xw4h4z">https://doi.org/10.7289/v5xw4h4z</a>
	Abbreviated as Florida (CRMP)

<p>Lamb, J. B., Williamson, D. H., Russ, G. R., &amp; Willis, B. L. (2015). Protected areas mitigate diseases of reef-building corals by reducing damage from fishing. <i>Ecology</i>, 96(9), 2555–2567.  <a href="https://doi.org/10.1890/14-1952.1">https://doi.org/10.1890/14-1952.1</a></p>	<p>Puerto Rico Department of Natural and Environmental Resources (2019). Puerto Rico Long-Term Coral Reef Monitoring Program database compilation: substrate cover percent, octocoral colony counts, macro invertebrate densities, fish densities, and fish biomass from 1999 to 2020 (NCEI Accession 0204647). [Data set]. NOAA National Centers for Environmental Information. Retrieved October 14, 2020, from  <a href="https://www.ncei.noaa.gov/archive/accession/0204647">https://www.ncei.noaa.gov/archive/accession/0204647</a></p> <p>Abbreviated as Puerto Rico (CRMP)</p>
<p>Page, C. A., Baker, D. M., Harvell, C. D., Golbuu, Y., Raymundo, L., Neale, S. J., Rosell, K. B., Rypien, K. L., Andras, J. P., &amp; Willis, B. L. (2009). Influence of marine reserves on coral disease prevalence. <i>Diseases of Aquatic Organisms</i>, 87(1–2), 135–150. <a href="https://doi.org/10.3354/dao02112">https://doi.org/10.3354/dao02112</a></p>	<p>Schumacher, B., Coral Reef Ecosystem Program Pacific Islands Fisheries Science Center (2015). Resilience of coral reefs in the main Hawaiian Islands from 2013 to 2014 (NCEI Accession 0128219). [Data set]. NOAA National Centers for Environmental Information.  <a href="https://www.ncei.noaa.gov/archive/accession/0128219">https://www.ncei.noaa.gov/archive/accession/0128219</a></p> <p>Abbreviated as Hawaii (2014)</p>
<p>Raymundo, L. J., Halford, A. R., Maypa, A. P., &amp; Kerr, A. M. (2009). Functionally diverse reef-fish communities ameliorate coral disease. <i>Proceedings of the National Academy of Sciences</i>, 106(40), 17067–17070.  <a href="https://doi.org/10.1073/pnas.0900365106">https://doi.org/10.1073/pnas.0900365106</a></p>	<p>Schumacher, B., Pacific Islands Fisheries Science Center Ecosystem Sciences Division (2018). Identifying coral reef resilience potential in Tutuila, American Samoa based on NOAA coral reef monitoring data from 2010 to 2016 (NCEI Accession 0169632). (Version 1) [Data set]. NOAA National Centers for Environmental Information.  <a href="https://www.ncei.noaa.gov/archive/accession/016963">https://www.ncei.noaa.gov/archive/accession/016963</a></p> <p>Abbreviated as American Samoa (2016)</p>
<p>Ruiz-Moreno, D., Willis, B., Page, A., Weil, E., Cróquer, A., Vargas-Angel, B., Jordan-Garza, A., Jordán-Dahlgren, E., Raymundo, L., &amp; Harvell, C. (2012a). Global coral disease prevalence associated</p>	<p>United States Environmental Protection Agency (2016). Biological status assessment of coral reefs in Southern Puerto Rico supporting coral reef protection under the U.S. Clean Water Act.</p>

with sea temperature anomalies and local factors. <i>Diseases of Aquatic Organisms</i> , 100(3), 249–261. <a href="https://doi.org/10.3354/dao02488">https://doi.org/10.3354/dao02488</a>	(Version 1) [Data set]. U.S. EPA Office of Research and Development (ORD) <a href="https://catalog.data.gov/dataset/2011-pr-survey-data">https://catalog.data.gov/dataset/2011-pr-survey-data</a>  Abbreviated as Puerto Rico (CWA)
van Woesik, R., & Burman, S. (2012). Coral bleaching, coral diseases, and protected areas in the Florida Keys (p. 23). The Nature Conservancy.	

**Appendix Table 3. Full citations of additional sources used to determine MPA status of cited sources.**

Source	MPA information source	MPA information source type
Bruckner (2010)	Ecoengineering Caribbean Limited. (2007). Carbits National Park (Marine Component) Site Report, Dominica (No. 11/2007; Eco Report, p. 318).	Report
Coehlo & Manfrino (2007)	Clark, T. (2013). Little Cayman Island Dive Map [GIS layer]. Esri.	Map/GIS layer
Lamb et al. (2016)	Great Barrier Reef Marine Park Authority. (2020). Great Barrier Reef Marine Park Zoning [GIS layer]. Esri.	Map/GIS layer
Lamb et al. (2015)	Great Barrier Reef Marine Park Authority. (2020). Great Barrier Reef Marine Park Zoning [GIS layer]. Esri.	Map/GIS layer

**Appendix Table 4. Full citations of sources excluded from the multiple comparison models (recalculated risk differences by MPA protection level or MPA age).**

Source
Hein, M. Y., Lamb, J. B., Scott, C., & Willis, B. L. (2015). Assessing baseline levels of coral health in a newly established marine protected area in a global scuba diving hotspot. <i>Marine Environmental Research</i> , 103, 56–65. <a href="https://doi.org/10.1016/j.marenvres.2014.11.008">https://doi.org/10.1016/j.marenvres.2014.11.008</a>
Page, C. A., Baker, D. M., Harvell, C. D., Golbuu, Y., Raymundo, L., Neale, S. J., Rosell, K. B., Rypien, K. L., Andras, J. P., & Willis, B. L. (2009). Influence of marine reserves on coral disease prevalence. <i>Diseases of Aquatic Organisms</i> , 87(1–2), 135–150. <a href="https://doi.org/10.3354/dao02112">https://doi.org/10.3354/dao02112</a>
Raymundo, L. J., Halford, A. R., Maypa, A. P., & Kerr, A. M. (2009). Functionally diverse reef-fish communities ameliorate coral disease. <i>Proceedings of the National</i>

*Academy of Sciences*, 106(40), 17067–17070.  
<https://doi.org/10.1073/pnas.0900365106>

**Appendix Table 5. Full citations of sources identified as outliers and removed from the general prevalence dataset, by method.**

<b>Studentized deleted residual method</b>	<b>Confidence interval method</b>
Coral Reef Ecosystem Program, Pacific Islands Fisheries Science Center (2018). Belt transect surveys of coral populations and disease assessments in Hawaii, Maui, and Oahu from 2010-03-08 to 2011-11-08 (NCEI Accession 0168912). (Version 1) [Data set]. NOAA National Centers for Environmental Information. <a href="https://accession.nodc.noaa.gov/0168912">https://accession.nodc.noaa.gov/0168912</a>	Coelho, V. R., & Manfrino, C. (2007). Coral community decline at a remote Caribbean island: Marine no-take reserves are not enough. <i>Aquatic Conservation: Marine and Freshwater Ecosystems</i> , 17(7), 666–685. <a href="https://doi.org/10.1002/aqc.822">https://doi.org/10.1002/aqc.822</a>
Hawai'i Coral Disease database (2004–2015). [Individual colony-level data of various surveys of Hawaiian coral reefs] [Unpublished data set]. NOAA National Centers for Environmental Information. <a href="https://www.ncei.noaa.gov/archive/accession/0128219">https://www.ncei.noaa.gov/archive/accession/0128219</a>	Coral Reef Ecosystem Program, Pacific Islands Fisheries Science Center (2018). Belt transect surveys of coral populations and disease assessments in Hawaii, Maui, and Oahu from 2010-03-08 to 2011-11-08 (NCEI Accession 0168912). (Version 1) [Data set]. NOAA National Centers for Environmental Information. <a href="https://accession.nodc.noaa.gov/0168912">https://accession.nodc.noaa.gov/0168912</a>
Hein, M. Y., Lamb, J. B., Scott, C., & Willis, B. L. (2015). Assessing baseline levels of coral health in a newly established marine protected area in a global scuba diving hotspot. <i>Marine Environmental Research</i> , 103, 56–65. <a href="https://doi.org/10.1016/j.marenvres.2014.11.008">https://doi.org/10.1016/j.marenvres.2014.11.008</a>	Hawai'i Coral Disease database (2004–2015). [Individual colony-level data of various surveys of Hawaiian coral reefs] [Unpublished data set]. NOAA National Centers for Environmental Information. <a href="https://www.ncei.noaa.gov/archive/accession/0128219">https://www.ncei.noaa.gov/archive/accession/0128219</a>
Lamb, J. B., Wenger, A. S., Devlin, M. J., Ceccarelli, D. M., Williamson, D. H., & Willis, B. L. (2016). Reserves as tools for alleviating impacts of marine disease. <i>Philosophical Transactions of the Royal Society B: Biological Sciences</i> , 371(1689). <a href="https://doi.org/10.1098/rstb.2015.0210">https://doi.org/10.1098/rstb.2015.0210</a>	Hein, M. Y., Lamb, J. B., Scott, C., & Willis, B. L. (2015). Assessing baseline levels of coral health in a newly established marine protected area in a global scuba diving hotspot. <i>Marine Environmental Research</i> , 103, 56–65. <a href="https://doi.org/10.1016/j.marenvres.2014.11.008">https://doi.org/10.1016/j.marenvres.2014.11.008</a>
Ruiz-Moreno, D., Willis, B., Page, A., Weil, E., Cróquer, A., Vargas-Angel, B., Jordan-Garza, A., Jordán-Dahlgren, E.,	Lamb, J. B., Wenger, A. S., Devlin, M. J., Ceccarelli, D. M., Williamson, D. H., & Willis, B. L. (2016). Reserves as tools for

Raymundo, L., & Harvell, C. (2012). Global coral disease prevalence associated with sea temperature anomalies and local factors. <i>Diseases of Aquatic Organisms</i> , 100(3), 249–261. <a href="https://doi.org/10.3354/dao02488">https://doi.org/10.3354/dao02488</a>	alleviating impacts of marine disease. <i>Philosophical Transactions of the Royal Society B: Biological Sciences</i> , 371(1689). <a href="https://doi.org/10.1098/rstb.2015.0210">https://doi.org/10.1098/rstb.2015.0210</a>
	Lamb, J. B., Williamson, D. H., Russ, G. R., & Willis, B. L. (2015). Protected areas mitigate diseases of reef-building corals by reducing damage from fishing. <i>Ecology</i> , 96(9), 2555–2567. <a href="https://doi.org/10.1890/14-1952.1">https://doi.org/10.1890/14-1952.1</a>
	Ruiz-Moreno, D., Willis, B., Page, A., Weil, E., Cróquer, A., Vargas-Angel, B., Jordan-Garza, A., Jordán-Dahlgren, E., Raymundo, L., & Harvell, C. (2012). Global coral disease prevalence associated with sea temperature anomalies and local factors. <i>Diseases of Aquatic Organisms</i> , 100(3), 249–261. <a href="https://doi.org/10.3354/dao02488">https://doi.org/10.3354/dao02488</a>

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## **BIOGRAPHY**

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