



Research article

Coral diversity matches marine park zonation but not economic value of coral reef sites at St. Eustatius, eastern Caribbean

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ABSTRACT

Stony corals play a key role in the marine biodiversity of many tropical coastal areas as suppliers of substrate, food and shelter for other reef organisms. Therefore, it is remarkable that coral diversity usually does not play a role in the planning of protected areas in coral reef areas. In the present study we examine how stony coral diversity patterns relate to marine park zonation and the economic value of reefs around St. Eustatius, a small island in the eastern Caribbean, with fisheries and tourism as important sources of income. The marine park contains two no-take reserves. A biodiversity survey was performed at 39 sites, 24 inside the reserves and 15 outside; 22 had a maximum depth >18 m and 17 were shallower. Data on economic value per site were obtained from the literature. Corals were photographed for the verification of identifications made in the field. Coral species richness ($n = 49$) was highest in the no-take reserves and species composition was mainly affected by maximum depth. No distinct relation is observed between coral diversity and fishery value or total economic value. Based on the outcome of this study we suggest that in future designs of marine park zonation in reef areas, coral diversity should be taken into consideration. This is best served by including reef areas with a continuous depth gradient from shallow flats to deep slopes.

1. Introduction

Coral reefs and their biota are threatened by global climate change and local human activities (Hughes et al., 2017, 2018; Heery et al., 2018). Coral bleaching as a result of rising sea water temperatures is considered to increase the worldwide extinction risk of coral species (Carpenter et al., 2008), whereas local loss of coral species is linked to immediate anthropogenic factors (Hoeksema and Koh, 2009; van der Meij et al., 2010). A common countermeasure against such human-induced threats is the establishment of Marine Protected Areas, MPAs (Bellwood et al., 2004). Although it is obvious that MPAs are designed to conserve or restore biodiversity (Zhao et al., 2020), it is usually not clear how species composition and species richness are used to define boundaries and zonation (Agardy et al., 2011; Pressey et al., 2015; Morzaria-Luna et al., 2018), including those in coral reef areas (Mellin et al., 2016). Possibly, the role of biodiversity in coral reef

ecosystem functioning is not always well understood or appreciated (Brandl et al., 2019).

Although in some studies, coral species composition plays a role in MPA planning (Beger et al., 2003; Guzman et al., 2004; Cortés-Useche et al., 2019), this is usually not the case, despite corals being the main constructors of reefs and many other species depending on them for food, shelter, or substrate (Patton, 1976; Scott, 1987; Howell et al., 2011; Stella et al., 2011; Hoeksema et al., 2012, 2022a, 2022c; Montano, 2020; Lymperaki et al., 2022; Maggioni et al., 2022). Typically, more emphasis is put on fish diversity in the design and management of MPAs in coral reef areas, predominantly because of its economic relevance in fisheries (Cinner et al., 2012; Edgar et al., 2014; Bayley et al., 2020; Weible et al., 2021) and its ecological role in relation to resilience (Bellwood et al., 2004; Mora et al., 2006; Emslie et al., 2015). The importance of fish diversity as a diving attraction may not always be taken into consideration here (Fabinyi, 2008), with the possible

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exception of large pelagic fishes and rare, cryptic fish species that live in sediment-rich environments close to coral reefs (Rudd and Tupper, 2002; Vianna et al., 2018; De Brauwer et al., 2019).

If no-take zones are designed to exclude fisheries, one would expect that the commercial harvesting or collecting of corals and other reef organisms would also be prohibited, even though this is usually not specifically mentioned (Miller et al., 2012; Roberts, 2012). This may explain why attention to corals in reef surveys is usually restricted in terms of cover and less of species diversity (e.g., Mumby and Harborne, 2010; Selig and Bruno, 2010; Brodie and Waterhouse, 2012; Ortiz Cajica et al., 2020; Wright, 2022). A problem in reef coral diversity data is that they can be biased towards well known species in the shallowest reef zones, while their taxonomy is not always consistent and up-to-date (Muir et al., 2022). Many coral diversity surveys are performed at depths down to 15 m (Aronson et al., 1994; Edinger et al., 1998; Yusuf et al., 2021) because these can be accessed more easily during SCUBA diving than deeper ones, due to air or nitrox supply and dive safety, although these reasons are usually not explained, or because the surveyed reefs simply lack deeper zones (Arulananthan et al., 2021; Ditzel et al., 2022).

If the protection of coral species is considered crucial in the management of reef biota, because corals are the foundation species of coral reef communities with other species depending on them (Stella et al., 2011; Tornabene et al., 2013; Ainsworth et al., 2020), it would be relevant to know whether coral diversity can indeed be linked to park zonation and no-take reserves make a difference herein. This information is not always utilized. For example, the Great Barrier Reef Marine Park (GBRMP) has a clear zonation plan, but it does not include the northernmost GBR reefs, which have the highest coral species richness (Fabricius and De'ath, 2008; Hoeksema, 2015). Such reefs are remote from human populations and experience less pressure than urban reefs (Heery et al., 2018). Owing to its huge size, the GBRMP requires a large-scale management that is incomparable with the running of small marine parks. Logistically, small parks may be easier to investigate as models regarding the conservation of biodiversity. A well-known example of a relatively small marine park is the Bonaire National Marine Park in the southern Caribbean, which was established in 1979 and includes two reserves where human entrance is prohibited (Thur, 2010; de Bakker et al., 2019).

An example of an even smaller and less-known marine park surrounds the volcanic island of St. Eustatius, in the eastern Caribbean (White et al., 2006). This park, the St. Eustatius National Marine Park (SNMP), includes two no-take reserves. In support of park management, the Dutch government supported recent surveys on marine habitats (Debrot et al., 2014), reef-fish assemblages (van Kuijk et al., 2015), fish biomass, reef health with coral cover, the abundance of key macro-invertebrates (de Graaf et al., 2015; Kitson-Walters, 2017), and the construction of artificial reefs (Hylkema et al., 2020). Coral-species occurrence around the island in previous studies was only included as a component of coral cover, which resulted in counts of 25 taxa in 2012–2013 (Debrot et al., 2014) and 30 taxa in 2017 (Kitson-Walters, 2017). The original management plan was proposed in a report that provided information on the marine resources of St. Eustatius, which was aimed at their sustainable use for tourism (Sybesma et al., 1993).

No survey has ever been undertaken on the number of coral species around St. Eustatius and how this species diversity is distributed. Consequently, it is unclear whether the park zonation is beneficial for the protection of benthic species diversity and threatened coral species. Therefore, we performed a survey to count coral species at a large number of sites around the island and analysed whether the total species number was sufficient to find diversity patterns matching the present park zonation. The results may indicate whether species diversity, next to park use, should play a balanced role in MPA zonation in other localities. Because coral species richness was not taken into consideration when the zonation of the marine park was planned (Sybesma et al., 1993) and also not after it became effective, we hypothesized that there

is no relation between coral species diversity pattern and the present marine park zonation at St. Eustatius, for which we used our own survey data. For the same reason we also hypothesized the absence of a relation between coral species richness and the economic value of reef sites, related to fisheries and other activities, for which we used data from the literature.

2. Material and methods

2.1. Research area

St. Eustatius (also known as Statia) is located in an island arc between the Caribbean Sea and the Atlantic Ocean. It is part of the Dutch Caribbean, and before October 10, 2010 one of the windward islands of the Netherlands Antilles (Hoeksema et al., 2017a). It is surrounded by St. Eustatius National Marine Park (SNMP), which covers the shelf area from the high-water mark down to the 30-m isobath (Fig. 1). The park was established in 1996 and has been managed by the St. Eustatius National Parks Foundation (STENAPA) since 1997 (White et al., 2006; MacRae and Esteban, 2007; McClellan, 2009). The park was established with various aims, including the conservation of marine biodiversity and marine productivity, the protection of fish stocks, and the limitation of pollution, in order to provide a foundation for a sustainable, nature-based tourism (MacRae and Esteban, 2007).

It covers an area of 27.5 km², divided over a general-use zone (22.6 km²) and two no-take reserves, one at northwestern section (1.6 km²) and one at the southwestern – southernmost section (3.3 km²). The goals of the reserves are to conserve marine biodiversity, protect fish stocks and promote sustainable tourism (MacRae and Esteban, 2007). SCUBA diving is allowed in and outside the no-take reserves. The purpose of the zonation is to conserve the coral reefs, while avoiding conflicts with users (Sybesma et al., 1993). In the reserves, coral reefs are protected by prohibiting anchoring as well as taking of invertebrates. Fishing would be allowed without spearfishing and with deployment of lobster traps only during the lobster season and not within 100 m radius from mooring buoys (Sybesma et al., 1993). Regarding the latter, the term “limited-take zone” might be more appropriate than “no-take reserve”. Outside the reserves, anchoring and shipping are less restricted, but there are specific anchoring zones (White et al., 2007). Fishing of sea turtles is also prohibited here (Smith, 2008). Beaches outside the park that are used by sea turtles are also monitored and protected (Berkel, 2012), but this has no relation with the coral reefs.

Both reserves are located at the leeward (Caribbean) side of the island. The remaining part of the MPA is a general-use zone that contains an oil terminal and a harbor. The oil terminal consists of 50 storage tanks (total capacity 1.75 10⁶ m³), three barges and a jetty with a capacity to serve two tankers at a time and a total of >1000 yr⁻¹, while anchoring takes place above depths of 24–40 m (White et al., 2007). Therefore, many activities of this terminal take place within the boundaries of the marine park and form a potential danger to the marine environment, especially by oil spills, sedimentation, turbidity, litter, chemicals, and shading (Sybesma et al., 1993; Slijkerman et al., 2016). In 2015, the park was rezoned: the Northern Reserve became part of the harbor area where anchoring is allowed, while the conditions for the Southern Reserve did not change (de Graaf et al., 2015).

2.2. Data sampling

The survey took place in June 7–27, 2015 during a marine biodiversity expedition at 39 localities, 37 of which were accessed by boat and two from the shoreline; 24 sites were situated inside the no-take reserves and 22 had a maximum depth of >18 m (Fig. 1; Hoeksema, 2016). Fourteen of the 22 deeper sites were located inside the reserves and eight were outside (Fig. 1). Stony corals were recorded and photographed by two divers at each site down to a maximum of 30 m depth, using the roving diver technique in order to score as many species as

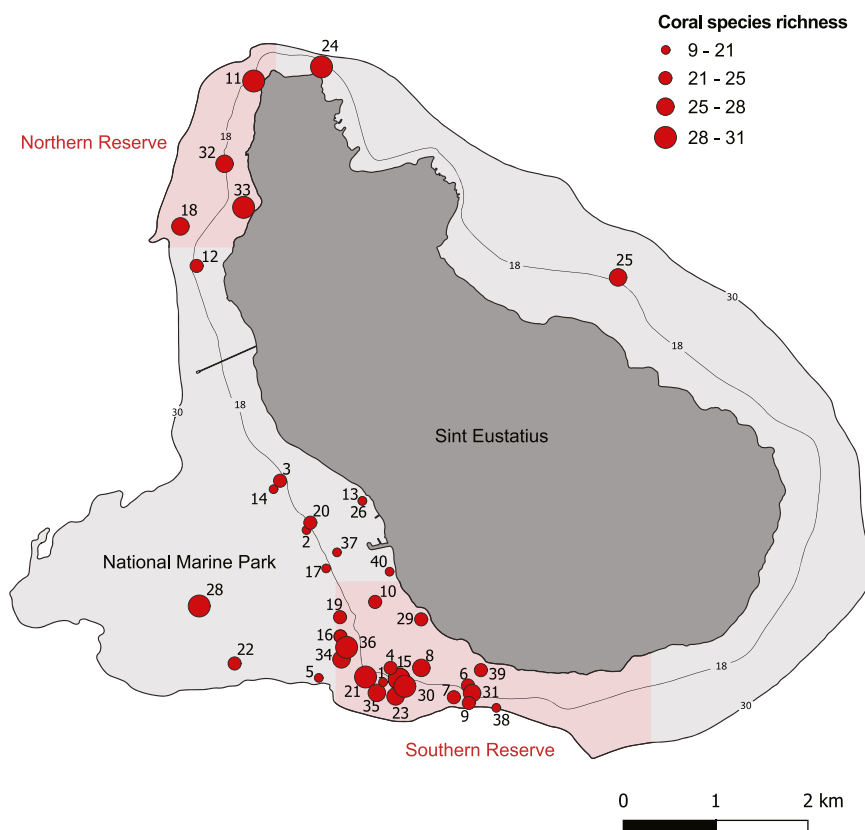


Fig. 1. Map of the coastal waters of St. Eustatius with 39 sample sites (numbered, red circles). Circle size corresponds with the number of coral species recorded per site. The St. Eustatius National Marine Park covers the shelf area from the high-water mark down to the 30-m isobath as outer boundary. In addition, the 18-m isobath is shown. The northern and southern no-take reserves are shaded pink and the rest of the park is shaded light grey. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

possible per dive of approximately 60 min, working upward from the maximum depth (Hoeksema and Koh, 2009). Most boat-dive localities were indicated by buoys as designated dive sites established by STEN-APA (Esteban, 2005). Per day no more than two dives were made.

Coral identities were confirmed with the help of various references (Zlatarski and Estalella, 1982; Collin et al., 2005; Reyes et al., 2010; Carballo-Bolaños et al., 2012; Bright and Lang, 2013; Humann and DeLoach, 2013). To avoid the use of invalid synonyms, the nomenclature was updated according to the World List of Scleractinia (of the World Register of Marine Species) (Hoeksema and Cairns, 2021). Per site, corals of each species were photographed for future verification, if possible. A selection of the photographs was mounted into panels to serve as reference document for all 49 recorded coral species used in the analyses (Electronic Supplementary Material ESM 1).

2.3. Alpha and beta diversity

Data on coral species richness and coral species composition per site were used to express alpha and beta diversity. Alpha diversity was measured as the number of coral species recorded per site and beta diversity as the variation in species among sample sites, based on several distance matrices (Section 2.5).

For both species richness and species composition, we tested if there were differences between sites: (1) located inside and outside the no-take reserves (Fig. 1); (2) with a maximum depth ≤ 18 m and > 18 m (Fig. 1), (3) with a fishery value of ≤ 70 USD $\text{ha}^{-1} \text{y}^{-1}$ and > 70 USD $\text{ha}^{-1} \text{y}^{-1}$ (Electronic Supplementary Material ESM 2 Fig. S50, ESM 3); (4) with a total economic value (TEV) ≤ 5000 USD $\text{ha}^{-1} \text{y}^{-1}$ and > 5000 USD $\text{ha}^{-1} \text{y}^{-1}$ (ESM 2 Fig. S51, ESM 3). Maximum depth (value 2) was recorded every dive using a diving computer and indicates the deepest point where observations were made, rather than the absolute maximum depth possible at the respective sites. To increase reliability, this variable was binned into a factor based on the median (≤ 18 m and > 18 m

depth). Values of (3) and (4) were taken from Tieskens et al. (2014). The fishery value was estimated using the value of various reef fish and lobster, allocated to marine habitats around St. Eustatius. Total economic value estimates were based on carbon sequestration, local cultural and recreational value, fisheries and tourism. Both fishery value and TEV were mapped to the 27.5 km^2 St. Eustatius National Marine Park using habitat zonation based on seascape video assessments by Debrot et al. (2014). Seascape habitat assessments were performed on a $150 \times 200 \text{ m}^2$ grid covering the entire marine park. For each of the dive sites in this study, we extracted the corresponding values (which were reported as categorical variables) from these maps. Statistical analyses were performed using R 3.5.1 (R Core Team, 2018).

2.4. Actual and expected species richness

A generalized linear model with a Poisson distribution was fitted to the data to test for differences in alpha diversity. The model allowed for a three-way interaction between maximum depth, presence of a reserve, and either fishery value or economic value. Non-significant interactions and terms were deleted from the model until a minimum adequate model was found. Model assumptions were graphically inspected using residual plots from the package car v.2.1-2 (Fox and Weisberg, 2011).

As coral species richness is hard to measure accurately, the observed species richness is usually lower than the true species richness, depending on the number of survey sites and the sampling effort per site (Hoeksema and Koh, 2009; Waheed and Hoeksema, 2013, 2014). To reduce the bias caused by under-sampling and estimate the asymptotic species richness, the estimators ICE (incidence coverage-based estimator) and the Chao2 index were calculated with EstimateS v.9.1.0 (Colwell, 2013). These estimators correct the observed species richness by adding a term based on the frequencies of species represented in one sample, in two samples or in a few samples (Gotelli and Colwell, 2010). Together, they provide a good range of the expected species richness. In

Table 1

Stony corals (Scleractinia, Milleporidae, Stylasteridae) recorded at St. Eustatius in 2015, and at Saba, Saba Bank, St. Eustatius, St. Maarten (SSSS) during other surveys: a) 1965 (Roos, 1971); b) 1972 (Bak, 1975); c) 1972 (van der Land, 1977); d) 2006 (McKenna and Etnoyer, 2010); e) 2011–2013 (van Beek and Meesters, 2013, 2014; Debrot et al., 2014); f) 2015 (Hoeksema et al., 2018; Hoeksema unpubl. data on Saba); g) 2017 (Kitson-Walters, 2017); h) 2019 (Homes, 2021). Records indicated by bold script letters indicate differences between the last two columns.

	St. Eustatius	SSSS (references a–g)
	2015	1965–2017
Anthozoa: Scleractinia		
Acroporidae		
<i>Acropora cervicornis</i> (Lamarck, 1816)	x	a, b, c, d, e, f, g
<i>Acropora palmata</i> (Lamarck, 1816)	x	a, b, c, f, h
<i>Acropora prolifera</i> (Lamarck, 1816)	x	
Agariciidae		
<i>Agaricia agaricites</i> (Linnaeus, 1758)	x	a, b, c, d, e, f, h
<i>Agaricia fragilis</i> Dana, 1846	x	e, f, h
<i>Agaricia grahamae</i> Wells, 1973		d, e
<i>Agaricia humilis</i> Verrill, 1901	x	d, e, f
<i>Agaricia lamarcki</i> Milne Edwards & Haime, 1851	x	d, e, f, h
<i>Agaricia tenuifolia</i> Dana, 1846		f
<i>Helioseris cucullata</i> (Ellis & Solander, 1786)	x	b, d, e, f
Astrocoeniidae		
<i>Stephanocoenia intersepta</i> (Esper, 1795)	x	a, b ¹ , c, d, e, f
Caryophylliidae		
<i>Colangia immersa</i> Pourtalès, 1871	x	f
<i>Rhizosmilia maculata</i> (Portalès, 1874)	x	
Dendrophylliidae		
<i>Tabastraea coccinea</i> Lesson, 1830	x	a ² , b, c ² , d, f, g ³
Faviidae: Faviinae		
<i>Colpophyllia breviserialis</i> Milne Edwards & Haime, 1849		e
<i>Colpophyllia natans</i> (Houttuyn, 1772)	x	a, b, c, d, e, f, g, h
<i>Diploria labyrinthiformis</i> (Linnaeus, 1758)	x	a, b, c, d, e, f, g, h
<i>Favia fragum</i> (Esper, 1795)	x	a, b, d, e ⁴ , g, h
<i>Manicina areolata</i> (Linnaeus, 1758)	x	a, b, c, d, e, g, h
<i>Pseudodiploria clivosa</i> (Ellis & Solander, 1786)	x	a ⁵ , b ⁵ , c ⁵ , e ⁵ , f, g, h ⁵
<i>Pseudodiploria strigosa</i> (Dana, 1846)	x	a ⁶ , b ⁶ , c ⁶ , d ⁶ , e ⁶ , f, g, h ⁶
Faviidae: Mussinae		
<i>Isophyllia rigida</i> (Dana, 1846)	x	a ⁷ , b ⁷ , c ⁷ , d ⁷ , e
<i>Isophyllia sinuosa</i> (Ellis & Solander, 1786)	x	a ⁸ , b ⁸ , c, d, e, f
<i>Mussa angulosa</i> (Pallas, 1766)	x	b, c, d, e, f
<i>Mycetophyllia aliciae</i> Wells, 1973	x	b, e, f
<i>Mycetophyllia danaana</i> Milne Edwards & Haime, 1849		e
<i>Mycetophyllia ferox</i> Wells, 1973		b, g, h
<i>Mycetophyllia lamarckiana</i> Milne Edwards & Haime, 1849		a, c, e, g
<i>Scolymia cubensis</i> (Milne Edwards & Haime, 1848)	x	b, e, f
<i>Scolymia lacera</i> (Pallas, 1766)	x	f, h
<i>Scolymia wellsi</i> Laborel, 1967		e
Meandrinidae		
<i>Dendrogyra cylindrus</i> (Ehrenberg, 1834)	x	b, c, d, e, f, h
<i>Dichocoenia stokesii</i> (Milne Edwards & Haime, 1849)	x	a, b, c, d, e ¹⁰ , f, g, h
<i>Eusmilia fastigiata</i> (Pallas, 1766)	x	a, b, c, d, e, f, g, h
<i>Meandrina danai</i> (Milne Edwards & Haime, 1848)	x	d ¹¹ , f
<i>Meandrina jacksoni</i> Weil & Pinzón, 2011	x	f, g
<i>Meandrina meandrites</i> (Linnaeus, 1758)	x	a, b, d, e, f, g, h
Merulinidae		
<i>Orbicella annularis</i> (Ellis & Solander, 1786)	x	a ¹² , b ¹² , c ¹² , d ¹² , e ¹² , f, g, h ¹²
<i>Orbicella faveolata</i> (Ellis & Solander, 1786)	x	d ¹³ , e, f, g, h ¹³
<i>Orbicella franksi</i> (Gregory, 1895)	x	d ¹⁴ , e ¹⁴ , f, g, h ¹⁴
Montastraeidae		
<i>Montastraea cavernosa</i> (Linnaeus, 1767)	x	a, b, c, d, e, f, h
Pocilloporidae		
<i>Madracis auretenra</i> Locke, Weil & Coates, 2007	x	b ¹⁵ , d, e ¹⁵ , f
<i>Madracis decactis</i> (Lyman, 1859)	x	a, b, d, e, f, g, h
<i>Madracis formosa</i> Wells, 1973		e
<i>Madracis pharensis</i> (Heller, 1868)	x	f
<i>Madracis senaria</i> Wells, 1973	x	f
Poritidae		
<i>Porites astreoides</i> Lamarck, 1816	x	a, b, c, d, e, f, g, h
<i>Porites branneri</i> Rathbun, 1888		h
<i>Porites divaricata</i> Le Sueur, 1820	x	d, e, f, g ¹⁶ , h
<i>Porites furcata</i> Lamarck, 1816	x	b, e, f, h
<i>Porites porites</i> (Pallas, 1766)	x	a, b, c, d, e, f, h
Rhizangiidae		
<i>Astrangia solitaria</i> (Le Sueur, 1818)	x	b, c
<i>Siderastrea radians</i> (Pallas, 1766)	x	a, b, c, f, g, h
<i>Siderastrea siderea</i> (Ellis & Solander, 1768)	x	a, b, d, e, f, g, h
Scleractinia incertae sedis		
<i>Cladocora arbuscula</i> (Le Sueur, 1820)		b

(continued on next page)

Table 1 (continued)

	St. Eustatius 2015	SSSS (references a–g) 1965–2017
<i>Solenastrea bourmoni</i> Milne Edwards & Haime, 1849	x	b, h
<i>Solenastrea hyades</i> (Dana, 1846)		e, g, h
Hydrozoa		
Milleporidae		
<i>Millepora alcornis</i> Linnaeus, 1758	x	a, c, d, e, f, h
<i>Millepora complanata</i> Lamarck, 1816	x	a, c, e, f, h
<i>Millepora squarrosa</i> Lamarck, 1816		c, e
Stylasteridae		
<i>Stylaster roseus</i> (Pallas, 1766)	x	f
Total number	49	59

Notes: species were originally recorded as: 1) *Stephanocoenia michelini* Milne Edwards & Haime, 1848; 2) *Tubastraea tenuilamellosa* (Milne Edwards & Haime, 1848); 3) *Tubastraea aurea* (Quoy & Gaimard, 1833); 4) *Favia leptophylla* Verrill, 1868 = *Mussimila leptophylla* (Verrill, 1868); 5) *Diploria clivosa* (Ellis & Solander, 1786); 6) *Diploria strigosa* (Dana, 1846); 7) *Isophyllastrea rigida* (Dana, 1846); 8) *Isophyllastrea sinuosa* (Ellis & Solander, 1786); 9) *Isophyllia multiflora* Verill, 1902; 10) *Dicho-coenia stellaris* Milne Edwards & Haime, 1848; 11) *Meandrina brasiliensis* (Milne Edwards & Haime, 1848); 12) *Montastrea annularis* (Ellis & Solander, 1786); 13) *Montastrea faveolata* (Ellis & Solander, 1786); 14) *Montastrea franki* (Gregory, 1895); 15) *Madracis mirabilis* (Duchassaing & Michelotti, 1860); 16) *Porites digitate* (misspelling).

addition, a species accumulation curve was generated to give an estimation of the effectivity of the sampling effort and of the number of samples required for a complete assessment (Colwell, 2013). If a horizontal level is reached in such a species accumulation curve, further sampling is not likely to yield additional species (Colwell et al., 2004).

2.5. Species composition: multivariate analyses

A principal component analysis (PCA) was performed using the Vegan v.2.3–5 package (Oksanen et al., 2016). In these plots, sites are scaled proportionally to eigenvalues, which means that distances among the dots representing a site are approximations of their Euclidean distances. Therefore, sites close to one another in the PCA plot are likely to have similar species compositions and species located close to a point representing a site are more likely to be found on that site (Legendre and Legendre, 2012). Singletons (species recorded only once) were excluded from the analyses. The remaining number of analysed species is 47.

A permutational analysis of variance (PERMANOVA), based on 10 000 permutations, was used to test for differences in species composition (Anderson, 2001). A PERMANOVA can be based on different distance matrices that taking beta diversity into account (Anderson et al., 2011). In this study, Jaccard, Euclidean, and Raup-Crick dissimilarities were used. Jaccard is one of the most widely used indices for presence-absence data and can be interpreted as the probability that two species, each drawn at random from two samples, will not be shared between these samples (Anderson et al., 2006). However, the Jaccard dissimilarity measure is not embedded in the Euclidean space and it does not take joint-absences into account, pertaining to species that are missing at both sites (Anderson et al., 2011). This means that sites are

not considered more similar if they both lack certain species. However, including joint-absences (using a Euclidean distance measure) can give additional information when testing hypotheses on the disappearance of species (e.g. in testing the effect of marine reserves or stochastic events). Both Jaccard and Euclidean distance measures depend at least to some extent on the alpha richness of the samples compared. The probabilistic Raup-Crick index depends on the number of species missing in both sites (Anderson et al., 2011), controlling for differences in alpha diversity. When *a* and *b* are the number of species on the compared sites and *c* the number of species occurring on both compared sites, the distance matrices are calculated using the *vegdist* function as follows (Oksanen et al., 2016):

$$\text{Jaccard dissimilarity} = (a + b - 2c) / (a + b - c)$$

$$\text{Euclidean dissimilarity} = \sqrt{a + b - 2c}$$

$$\text{Raup - Crick dissimilarity} = 1 - \text{prob}(c)$$

The PERMANOVA model allowed for a three-way interaction between maximum depth, presence of a reserve, and either economic or fishery value. Non-significant interactions and terms were sequentially deleted from the model until a minimum adequate model was found. A PERMANOVA assumes that the multivariate spread is equal among groups. This was tested with the *betadisper* function and with the visual

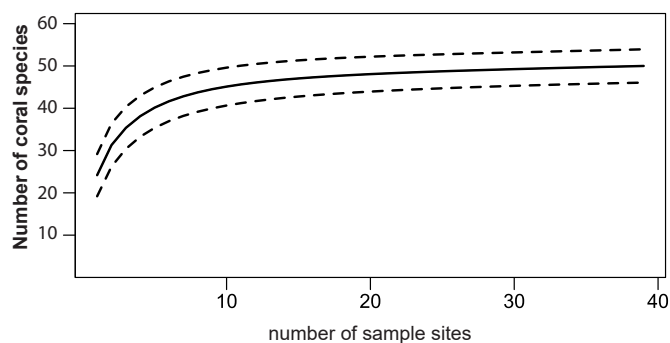


Fig. 2. Sample-based rarefaction curve with the Mau Tao estimator of expected richness (solid curve) and 95% confidence intervals (dashed curves).

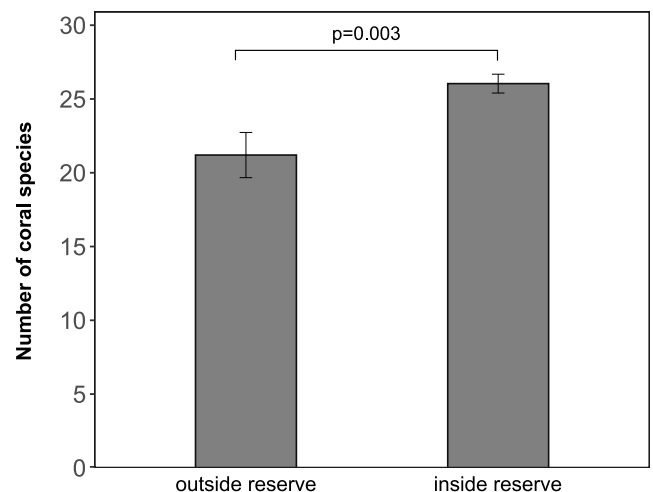


Fig. 3. Bar plot with observed species richness at sample sites located outside and inside the no-take reserves. Data are displayed as mean ± SE.

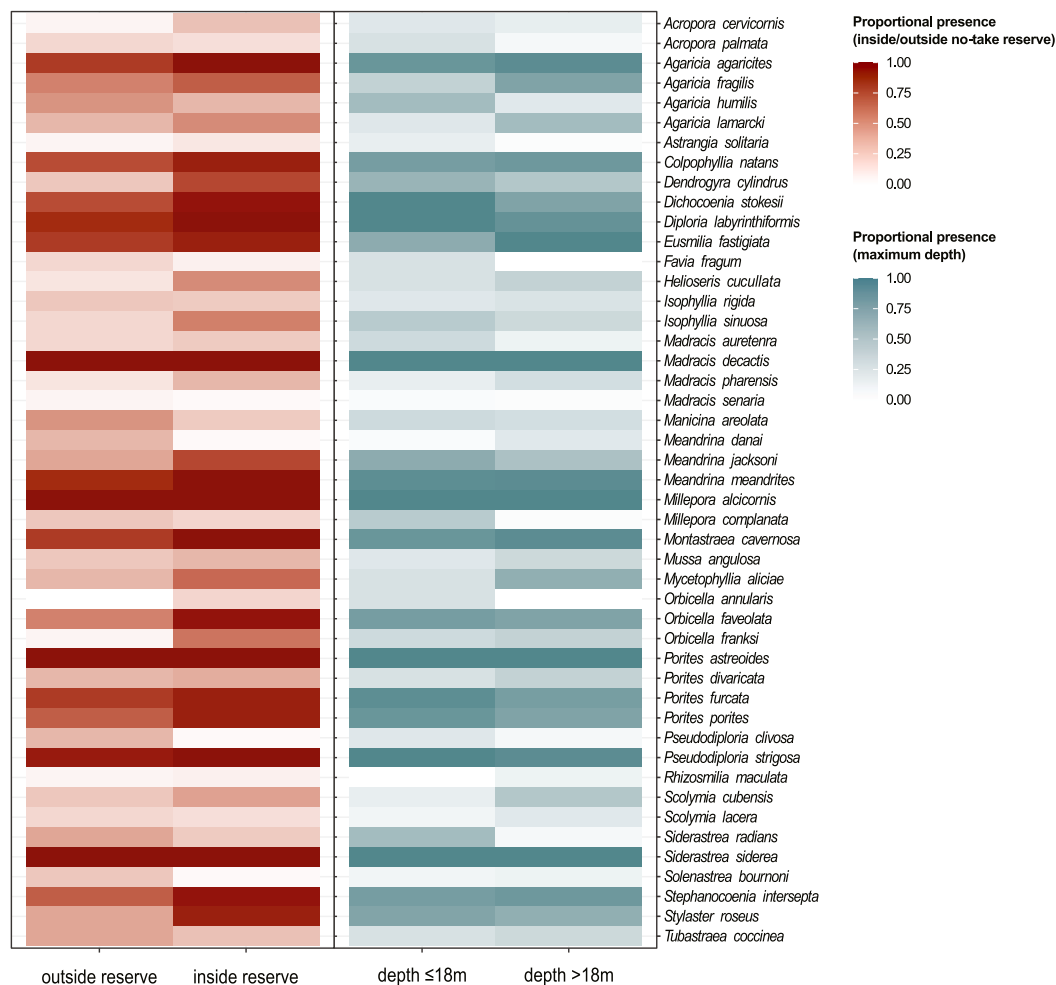


Fig. 4. Heatmap showing proportional presence of coral species in-and outside the no-take reserves (red bars) and in relation to maximum depth (blue bars). Colours vary from 1.00 with the species present in 100% of the sites, to 0.00 with species absent at all sites. For example, *Orbicella annularis* was absent in all sites outside the reserve and at all sites with max. depth >18 m, but could be found in 21% of the sites located within the no-take reserves, and in 30% of the shallow sites. Overall, the sites inside the reserves showed a higher presence of species than those outside. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

inspection of dispersion plots (Anderson, 2006; Oksanen et al., 2016).

3. Results

3.1. Species richness (alpha diversity) and expected species richness

In total, 49 stony coral species were recorded, including 46 scleractinians, two milleporids and one stylasterid (Table 1; Electronic Supplementary Material ESM 1). The present records were compared with those of other reef surveys in the eastern Dutch Caribbean (the former windward Netherlands Antilles), which were executed in the period 1965–2017 and showed a total of 59 species (Table 1). The new records made in 2015 only concerned *Acropora prolifera* and *Rhizosmilia maculata*. Various species that were not retrieved are discussed later (Section 4.4).

Accumulation curves for the species numbers increased steadily over the first ten sample locations and approached a horizontal asymptote after approximately 27 (of 39) sample locations (Fig. 2). This indicated that 27 dives were sufficient to sample the full coral species assemblage around St. Eustatius. The expected species richness based on the ICE estimator was 51 ± 0 and based on the Chao2 estimator 51 ± 2.5 .

Poisson regressions showed that maximum depth ($p = 0.973$), total economic value ($p = 0.715$) and fisheries value ($p = 0.409$) were not

significantly correlated with observed coral species richness (data in Electronic Supplementary Material ESM 2). However, marine park zonation was significantly linked to increased stony coral species diversity ($p = 0.003$; Poisson model). The mean number of observed species on sites situated within a no-take reserve (26 ± 0.6 SE) was higher than on sites located outside the reserves (21 ± 1.5 SE) (Fig. 3).

3.2. Species composition: multivariate analyses

Acropora prolifera (<2 m depth outside the reserves) and *Colangia immersa* (>18 m depth inside a reserve) were singletons and excluded from the multivariate analysis; therefore, the number of analysed coral species is 47 instead of the 49 listed in Table 1. All recorded coral species were found inside the reserves (24 sites) and all but one outside the reserve (15 sites), the missing one being the shallow-water coral *Orbicella annularis* (Electronic Supplementary Material ESM 4; Fig. 4). The azooxanthellate coral *Rhizosmilia maculata* was not found at the 17 shallow sites (≤ 18 m) and the zooxanthellate species *Favia fragum* and *Orbicella annularis* were not observed at the 22 deeper sites (>18 m; Fig. 4; Electronic Supplementary Material ESM 5). Four species were found at all dive sites: *Madracis decactis*, *Millepora alcicornis*, *Porites astreoides*, and *Siderastrea siderea* (Fig. 4).

Results of the PCA for coral species composition data showed a

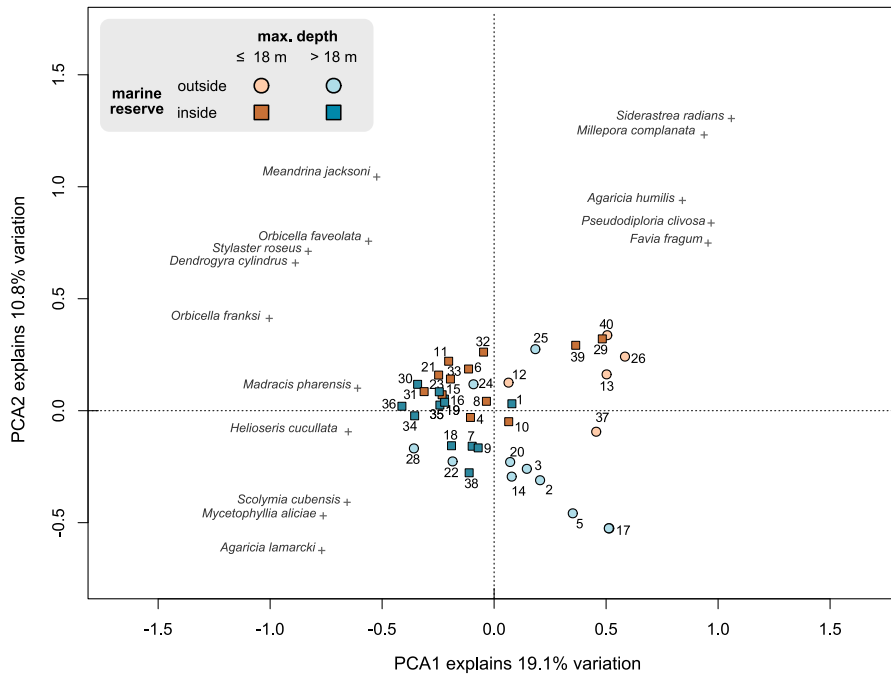


Fig. 5. Principal component analysis (PCA) visualization of coral fauna compositions comparing sites inside reserves with those outside, and sites at shallow sites (max. depth ≤ 18 m) and deep sites (max. depth > 18 m). Indicator species explaining most of the variability are mentioned.

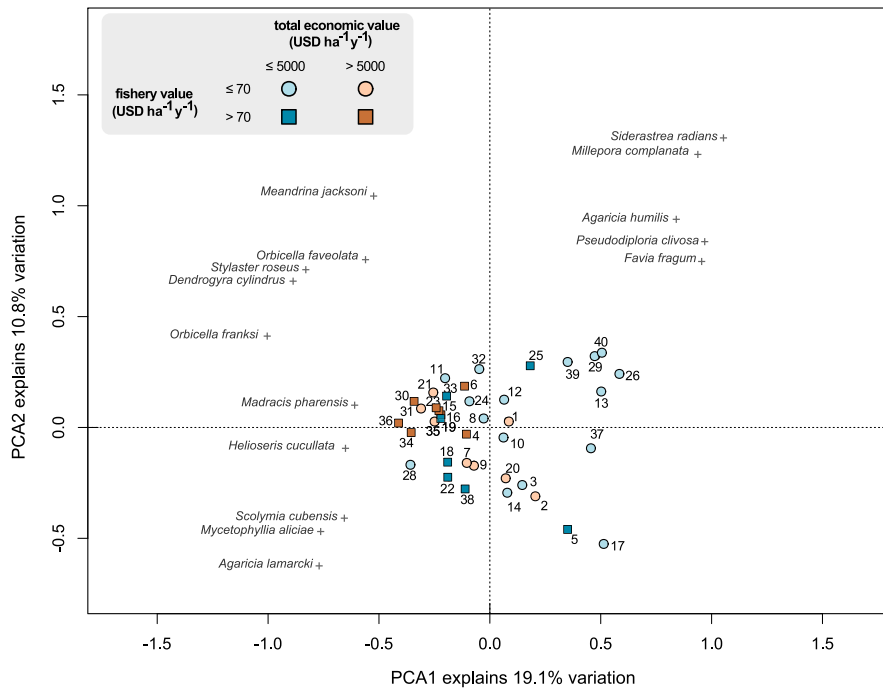


Fig. 6. Principal component analysis (PCA) visualization of coral species composition, with sites that have an estimated fishery value of ≤ 70 USD $\text{ha}^{-1} \text{y}^{-1}$ and sites that have an estimated fishery value of > 70 USD $\text{ha}^{-1} \text{y}^{-1}$, as well as sites that have an estimated total economic value of ≤ 5000 USD $\text{ha}^{-1} \text{y}^{-1}$ and the sites that have an estimated total economic value of > 5000 USD $\text{ha}^{-1} \text{y}^{-1}$. No significant distinctions can be seen between values (Table 2).

separation between sites located inside and outside a reserve, and between sites with a maximum depth ≤ 18 m versus maximum depth > 18 m (Fig. 5). The variation in the presence of a marine reserve is mainly expressed across the horizontal PCA axis (most of the sites located outside the reserve clustered towards the right of the plot, whereas most of the sites located within the reserves were clustered towards the left) (Fig. 5). Variation across maximum depth is mainly expressed across the

second axis (vertical axis), as most shallow sites clustered towards the top and the deeper sites clustered towards the bottom (Fig. 5). No distinct pattern can be observed between coral species composition with either fishery value or total economic value (Fig. 6).

Results from the PERMANOVA yielded similar observations: total economic value and fishery value did not significantly affect coral species composition based on any of the three dissimilarity indices (Jaccard,

Table 2

Statistics (F-value, R^2 , and permutational p-value) of a PERMANOVA with 10,000 permutations used for F-tests based on coral species beta diversity related to associated environmental variables (fishery value, total economic value, maximum depth and the presence of a no-take reserve; Electronic Supplementary Material ESM 2–5) using three dissimilarity indices: Jaccard, Euclidean and Raup-Crick. P-values of individual factors are not reported if they participate in a significant interaction. * Significant values are printed in bold.

Factor	Jaccard			Euclidean			Raup-Crick		
	R^2	F model	p-value	R^2	F model	p-value	R^2	F model	p-value
Maximum depth: no-take reserve (interaction)	0.06	2.84	0.004	0.04	1.79	0.029	0.09	10.00	0.06
Maximum depth	–	–	–	–	–	–	0.49	56.55	<0.001
No-take reserve	–	–	–	–	–	–	1.00	11.28	0.075
Fishery value	0.02	0.88	0.552	0.02	1.01	0.416	0.07	7.80	0.136
Total economic value	0.03	1.58	0.103	0.03	1.48	0.084	–0.03	–3.75	0.864
Residuals	0.69	–	–	0.75	–	–	0.29	–	–

Euclidean, and Raup-Crick) ($p > 0.05$, Table 2). Both maximum depth and marine reserve boundaries significantly affected species composition based on the Jaccard and Euclidean distances ($p < 0.01$ and $p < 0.03$, Table 2). However, based on the Raup-Crick dissimilarity index, only maximum depth had a significant effect ($p < 0.001$, Table 2), as that of no-take reserve presence was marginally non-significant ($p = 0.075$, Table 2).

Distinguishing species (explaining most of the variability in the PCA) included, in order of decreasing importance: *Siderastrea radians*, *Orbicella franksi*, *Dendrogyra cylindrus*, *Millepora complanata*, *Stylaster roseus*, *Meandrina jacksoni*, *Agaricia lamarcki*, *Mycetophyllia aliciae*, *Orbicella faveolata*, *Favia fragum*, *Agaricia humilis*, *Pseudodiploria clivosa*, *Helioseris cucullata*, *Madracis pharensis* and *Scolymia cubensis* (Figs. 5 and 6). Of these species, *D. cylindrus*, *S. roseus*, *M. aliciae*, *O. faveolata*, *H. cucullata*, and *M. pharensis* were found most frequently at sites inside a marine reserve (Fig. 4). *Orbicella franksi* was even observed almost exclusively inside reserves. On the other hand, the shallow-water species *Siderastrea radians* and *Pseudodiploria clivosa* were found more frequently outside the reserves (Fig. 4). *Agaricia lamarcki*, *Madracis pharensis*, *Mycetophyllia aliciae*, and *S. cubensis* were most commonly recorded at deeper sites (max. depth > 18 m), whereas *S. radians*, *M. complanata*, *F. fragum*, *A. humilis*, and *P. clivosa* were predominantly found at shallow sites (max. depth ≤ 18 m) (Fig. 4).

There are some remarkable records, which were rare and did not contribute substantially to the variability of the PCA, or not at all. One of these is *Acropora prolifera* as a new record for St. Eustatius (Table 1), which was found in very shallow water (< 2 m depth) at a single locality near the shoreline and outside the reserves. As a singleton it was not included in the PCA. Because most dives were offshore, the shallow-water species *Favia fragum* and *Pseudodiploria clivosa* were only recorded five and six times, respectively. The free-living species *Manicina areolata* and *Meandrina danai* were found in both depth categories, inside and outside the reserves, and also did not contribute to the variability of the PCA (Fig. 5).

4. Discussion

4.1. Coral species diversity pattern in relation to park zonation

An important outcome of this study is that the species richness of stony corals at St. Eustatius is significantly higher at dive localities situated inside the reserves than at those outside. Because corals are the main reef builders and many other reef-dwelling species depend on them for their existence (Stella et al., 2011), it is important that their diversity is optimally covered by MPA zonation. In St. Eustatius, the local presence of lava flows as foundation for coral growth is important herein because of their rugosity, which support reef communities, even in water less than 4 m deep (Hill et al., 2021; Hoeksema and ten Hove, 2017; Lymperaki et al., 2022).

Fisheries management was originally considered the most important reason for the establishment of the marine reserves of St. Eustatius

(White et al., 2006), while coral diversity has so far not been considered for the park design. Nevertheless, the complexity of habitat structure is viewed of paramount importance for the local fish assemblages (van Kuijk et al., 2015) and elsewhere (Hackradt et al., 2011; Rees et al., 2018). Since stony corals are important contributors in the formation of this habitat structure, it is relevant to consider that coral species composition may be an important factor herein, in addition to coral cover (Öhman and Rajasuriya, 1998; Komyakova et al., 2013; Chaput et al., 2019). A higher coral diversity supports a higher fish species diversity, although this may predominantly benefit small-bodied and relative rare fish species (Brandl et al., 2018; Richardson et al., 2017; Cardoso et al., 2020). These small species are also important in the food web of reefs (Brandl et al., 2019), where they find shelter in worm holes or between coral branches and tentacles. This is well studied on Indo-Pacific reefs (Tornabene et al., 2013; Wilson et al., 2013; Bos and Hoeksema, 2015) but less so in the Caribbean, except for the general reef environment, depth, and microhabitats (Greenfield and Johnson, 1999; Harborne et al., 2012; Böhm and Hoeksema, 2017). As for St. Eustatius, fish censuses are relatively poor in cryptobenthic species, which is likely related to an observation bias (Davies and Piontek, 2017; Robertson et al., 2020).

Although coral species composition (beta diversity) differed both with no-take reserves as well as maximum depth based on a Jaccard and Euclidean distance matrix, the Raup-Crick distance matrix only showed differences in species composition with maximum depth. Both Jaccard and Euclidean distance matrices depend to some extent on species richness (alpha diversity), whereas Raup-Crick (a probabilistic index) controls for differences in alpha diversity. This indicates that species richness patterns are largely different in- and outside marine reserve boundaries, and species composition is mainly affected by maximum depth. In total, PCA axis 1 and 2 explained 30% of the variation. As coral reef habitats are complex ecosystems, additional environmental factors are likely to play a role in species richness and composition.

4.2. Coral species richness pattern in relation to economic value

Not all commercial fish species in coral reef areas depend on reef corals and especially not on coral species composition when pelagics are considered (Arai, 2015). This may explain why no distinct relation was observed between fisheries value and coral fauna. The relation between fish diversity and coral diversity needs further investigation, stressing the difference between species with and without commercial importance. On the other hand, since fisheries is forbidden in the no-take reserves and a relation between species composition and zonation was found, a relation between coral species composition and fisheries value cannot be excluded.

The total economic value of dive sites does not show a relation with coral species composition as well. The total economic value also involves income from dive tourism, which benefits from coral reef diversity. However, dive operators usually do not consider coral fauna composition in their selection of dive sites but instead value specific

attractions, such as ship wrecks, archeological objects, and iconic or rare species. The latter could be important for underwater photographers who look for small, cryptic species (Uyarra and Côté, 2007; De Brauwer et al., 2017; Giglio et al., 2018). Eventually, the choice of dive sites may depend on how diving tourists perceive environmental quality (Petrosillo et al., 2007) and most of them may not have an adequate idea of biodiversity (Spash, 2000).

4.3. Variation in coral diversity

The species number observed in the present survey (49 stony corals, including 46 scleractinians) is not easily compared with species numbers found in other Caribbean areas, such as the leeward islands of the southern Dutch Caribbean with 57 scleractinians (Bak, 1975) and Yucatan, Mexico, also in the southern Caribbean, with 41 scleractinians (Ward et al., 2006). Although the reefs in the eastern (windward) Caribbean are considered less developed and poorer in species than those in the southern (leeward) Caribbean (Bak, 1975, 1977), it appears that much of the spatial and temporal variation in recorded coral species richness in the Caribbean depends on the inclusion of small azooxanthellate corals, whose species names were considered valid or invalid at the time of recording, and on possible misidentifications (Table 1). Most of the azooxanthellate coral species at depths <30 m are cryptic by being small, hidden and uncommon (Cairns, 2000; Santodomingo et al., 2013). Therefore, they can easily be missed during reef surveys. For instance, the absence of the azooxanthellate coral species *Phyllangia americana* Milne Edwards and Haime, 1849 (Table 1), is remarkable, since it is commonly found in the Caribbean, especially on manmade substrates (Cairns, 2000; Durán-Fuentes et al., 2021). Also, the recognition of some zooxanthellate species, such as several *Madracis* species, requires close inspection.

Based on earlier surveys and the present results, the list of species records from the eastern Dutch Caribbean totals up to 61, including two new ones. The record of 49 from the present survey is much lower than the total of 59 of the other ones (Table 1). This gap is partly due to different opinions regarding species identifications (Cortés-Useche et al., 2019). Indeed, there still is uncertainty in the identity and distribution of some Caribbean and other Atlantic reef coral species (Prada et al., 2014; De Souza et al., 2017; Hoeksema et al., 2019b). An integrative molecular-morphological approach may help to solve such species problems (Kitahara et al., 2016), such as in the genus *Mycetophyllia* Milne Edwards & Haime 1848. This genus consists of five extant species (Hoeksema and Cairns, 2021), four of which were previously recorded from the eastern Caribbean, while in the present survey only *M. aliciae* was found (Table 1).

Some records of the genus *Scolymia* Haime 1852, with three extant species (Hoeksema and Cairns, 2021), are also disputable. *Scolymia wellsi* is originally described from Brazil and therefore its previous record from the eastern Caribbean (Table 1) and other Caribbean localities is uncertain (e.g. Zlatarski and Estalella, 1982; Collin et al., 2005; Carballo-Bolaños et al., 2012; Humann and DeLoach, 2013). Due to the similarity between juvenile *Mussa angulosa* and *Scolymia* spp. (Fenner, 1993; Neves et al., 2006), it is possible that some of the earlier records of *Scolymia* species concern *Mussa angulosa*. *Mussismilia leptophylla* (Verrill, 1868), previously reported from Saba Bank as *Favia leptophylla* (Table 1), is also endemic to Brazil (Nunes et al., 2008). This erroneous historical record may be based on a misidentified *Dichocoenia stokesii*.

Acropora prolifera, which was found in very shallow water, represents a new record for St. Eustatius (Table 1, Electronic Supplementary Material ESM 1 Fig. S3). However, it is not new for the eastern Caribbean (Japaud et al., 2014). *Acropora prolifera* is actually a hybrid form of *A. cervicornis* and *A. palmata*, but it is treated as a taxon of its own with the capacity to live in sediment-rich environments (Japaud et al., 2014; Aguilar-Perera and Hernández-Landa, 2018; Zlatarski and Greenstein, 2020). Perhaps particular conditions allow this shallow-water taxon to increase its abundance and densities, which may explain the present

new record at St. Eustatius. Another explanation is that shallow reef zones (<4 m depth) are not surveyed sufficiently. Some common species, such as *Siderastrea radians* and *Pseudodiploria clivosa*, both typical for shallow depths at St. Eustatius (Hill et al., 2021), were also found most frequently outside the reserves (Electronic Supplementary Material ESM 4).

Among coral species that were representative for the two no-take reserves, *Helioseris cucullata* stood out by being common at St. Eustatius (14 out of 39 sites, 12 inside reserves). At other Caribbean localities declines in abundance of this species have been observed in the last two decades (Hughes and Tanner, 2000; Vermeij et al., 2011; Miller et al., 2016). This species has a relatively rich associated fauna at St. Eustatius (Hoeksema et al., 2017b, 2022b) and is competitive in interactions with sponges (García-Hernández et al., 2017). Protection of its population is served by maintaining the present park zonation at St. Eustatius.

4.4. Importance of depth range in reef conservation strategies

The difference in coral species composition between shallow reefs (maximum depth ≤18 m) and reefs with maximum depths >18 m implies that for conserving maximum species diversity, both shallow and deep reef habitats should be included in the reserves. At St. Eustatius, the shallow reef environments are nearshore, whereas the deep ones are more remote and only accessible by boat. For instance, *Favia fragum* and *Pseudodiploria clivosa* are common at wave-exposed reefs less than 4 m deep (Hoeksema et al., 2020; Hill et al., 2021). On the other hand, all records of the free-living coral *Meandrina danai* came from depths >18 m, where it usually occurs on flat, sandy substrates (Meesters et al., 2013; Hoeksema et al., 2018). Depth and substrate were also an important factor for the distribution of algae around St. Eustatius. This makes sense because like corals, they also depend on light, wave action and type of seabed (van der Loos et al., 2017).

To be rich in coral species, a site should ideally have a depth profile ranging from shallow reef flats to deep slopes, like at Saba (the island adjacent to St. Eustatius), where 42 stony coral species were observed during nine dives in a depth interval from 1 to 30 m at a single site (Ladder Bay at 7°37'34"N 63°15'37"W, November 2015; Table 1). The importance of bathymetric range as a contributing factor to habitat diversity has also been found in other reef coral diversity studies (Huston, 1985; Cleary et al., 2005; Hoeksema and Giyanto, 2019a; Roberts et al., 2019). This factor should therefore preferably be considered in the planning of marine park zonation.

5. Conclusions

The present study examines the relation of coral diversity patterns and marine park zonation and the economic value of reefs around St. Eustatius, a small island in the eastern Caribbean, with fisheries and tourism as sources of income. Coral species richness was highest in no-take reserves and species composition was mainly affected by maximum diving depth.

Coral species richness is usually not considered in the design of MPAs in reef areas, which are known for their high marine biodiversity (Hoeksema, 2007; Plaisance et al., 2011) and need for conservation (Huang et al., 2016; Asaad et al., 2018). The present study, which is based on one month of fieldwork, shows (in retrospect) that coral diversity could have been used as a contributing element in the design of Statia's MPA zonation. This is supported by the role of corals in providing food, shelter and substrate to other reef species.

Therefore, it is recommended that in the future design of marine park zonation in reef areas, coral diversity should be taken into consideration (Becking et al., 2006; Cleary et al., 2006; Waheed et al., 2015). This is best served by including areas with environmental gradients that vary in wave exposure, depth, and sedimentation (Cleary et al., 2005; Gittenberger et al., 2015).

Coral diversity appears not to be linked the economic value of

individual dive sites. With regard to the profitability of the diving industry, this may not be relevant because diving tourists usually aim for variation of dive sites and underwater landscapes in the entire area that they visit. Our hypothesis that there is no relation between coral diversity patterns and the marine park zonation at St. Eustatius is rejected. The hypothesis that there is no relation between coral diversity patterns and the economic value of reef sites could not be rejected.

Credit authorship contribution statement

Bert W. Hoeksema: Investigation, Writing – original draft, Writing – review & editing, Visualization. Luna M. van der Loos: Investigation, Writing – original draft, Writing – review & editing, Visualization. Godfried W.N.M. van Moorsel: Investigation, Writing – review & editing, Visualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data are submitted as ESM

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jenvman.2022.115829>.

Electronic Supplementary Material.

ESM 1. Photographic guide of 49 coral species encountered at St. Eustatius in 2015.

ESM 2. Maps indication economic value of localities in the Marine Park of St. Eustatius.

ESM 3. Environmental data of 39 dive sites around St. Eustatius.

ESM 4. Presence/absence of coral species inside and outside reserves.

ESM 5. Presence/absence of coral species in two depths zones: ≤ 18 m and > 18 m.

References

- Agardy, T., di Sciara, G.N., Christie, O., 2011. Mind the gap: addressing the shortcomings of marine protected areas through large scale marine spatial planning. *Mar. Pol.* 35, 226–232. <https://doi.org/10.1016/j.marpol.2010.10.006>.
- Aguiar-Perera, A., Hernández-Landa, R.C., 2018. Occurrence of large thickets of *Acropora prolifera* (Scleractinia: acroporidae) in the southern gulf of Mexico. *Mar. Biodivers.* 48, 2203–2205. <https://doi.org/10.1007/s12526-017-0685-4>.
- Ainsworth, T.D., Renzi, J.J., Silliman, B.R., 2020. Positive interactions in the coral macro and microbiome. *Trends Microbiol.* 28, 602–604. <https://doi.org/10.1016/j.tim.2020.02.009>.
- Anderson, M.J., 2001. A new method for non-parametric multivariate analysis of variance. *Austral. Ecol.* 26, 32–46. <https://doi.org/10.1111/j.1442-9993.2001.01070>.
- Anderson, M.J., 2006. Distance-based tests for homogeneity of multivariate dispersions. *Biometrics* 62, 245–253. <https://doi.org/10.1111/j.1541-0420.2005.00440.x>.
- Anderson, M.J., Ellingsen, K.E., McArdle, B.H., 2006. Multivariate dispersion as a measure of beta diversity. *Ecol. Lett.* 9, 683–693. <https://doi.org/10.1111/j.1461-0248.2006.00926.x>.
- Anderson, M.J., Crist, T.O., Chase, J.M., Vellend, M., Inouye, B.D., Freestone, A.L., et al., 2011. Navigating the multiple meanings of β diversity: a roadmap for the practicing ecologist. *Ecol. Lett.* 14, 19–28. <https://doi.org/10.1111/j.1461-0248.2010.01552.x>.
- Arai, T., 2015. Diversity and conservation of coral reef fishes in the Malaysian South China Sea. *Rev. Fish Biol. Fish.* 25, 85–101. <https://doi.org/10.1007/s11160-014-9371-9>.
- Aronson, R.B., Edmunds, P.J., Precht, W.F., Swanson, D.W., Levitan, D.R., 1994. Large-scale, long-term monitoring of Caribbean coral reefs: simple, quick, inexpensive techniques. *Atoll Res. Bull.* 421, 1–19.
- Arulananthan, A., Herath, V., Kuganathan, S., Upasanta, A., Harishchandra, A., 2021. The status of the coral reefs of the Jaffna Peninsula (northern Sri Lanka), with 36 coral species new to Sri Lanka confirmed by DNA bar-coding. *Oceans* 2, 509–529. <https://doi.org/10.3390/oceans2030029>.
- Asaad, I., Lundquist, C.J., Erdmann, M.V., Costello, M.J., 2018. Delineating priority areas for marine biodiversity conservation in the Coral Triangle. *Biol. Conserv.* 222, 198–211. <https://doi.org/10.1016/j.biocon.2018.03.037>.
- Bak, R.P.M., 1975. Ecological aspects of the distribution of reef corals in The Netherlands Antilles. *Bijdr. Dierk* 45, 181–190. <https://doi.org/10.1163/26660644-04502002>.
- Bak, R.P.M., 1977. Coral reefs and their zonation in Netherlands Antilles: modern and ancient reefs. *AAPG Stud. Geol.* 4, 3–16.
- Bayley, D.T.I., Purvis, A., Nellas, A.C., Arias, M., Koldewey, H.J., 2020. Measuring the long-term success of small-scale marine protected areas in a Philippine reef fishery. *Coral Reefs* 39, 1591–1604. <https://doi.org/10.1007/s00338-020-01987-7>.
- Becking, L.E., Cleary, D.F., de Voogd, N.J., Renema, W., de Beer, M., van Soest, R.W.M., et al., 2006. Beta diversity of tropical marine benthic assemblages in the Spermonde Archipelago, Indonesia. *Mar. Ecol. Prog. Ser.* 27, 76–88. <https://doi.org/10.1111/j.1439-0485.2005.00051.x>.
- Beger, M., Jones, G.P., Munday, P.L., 2003. Conservation of coral reef biodiversity: a comparison of reserve selection procedures for corals and fishes. *Biol. Conserv.* 111, 53–62. [https://doi.org/10.1016/S0006-3207\(02\)00249-5](https://doi.org/10.1016/S0006-3207(02)00249-5).
- Bellwood, D.R., Hughes, T.P., Folke, C., Nystrom, M., 2004. Confronting the coral reef crisis. *Nature* 429, 827–833. <https://doi.org/10.1038/nature02691>.
- Berkel, J., 2012. St. Eustatius National Parks Foundation Sea Turtle Conservation Program. Annual Report 2012. St. Oranjestad. Eustatius National Parks Foundation, p. 61.
- Böhm, T., Hoeksema, B.W., 2017. Habitat selection of the coral-dwelling spinyhead blenny, *Acanthemblemaria spinosa*, at Curaçao, Dutch Caribbean. *Mar. Biodivers.* 47, 17–25. <https://doi.org/10.1007/s12526-016-0543-9>.
- Bos, A.R., Hoeksema, B.W., 2015. Cryptobenthic fishes and co-inhabiting shrimps associated with the mushroom coral *Heliopora actiniformis* (Fungiidae) in the Davao Gulf, Philippines. *Environ. Biol. Fish.* 98, 1479–1489. <https://doi.org/10.1007/s10641-014-0374-0>.
- Brandl, S.J., Goatley, C.H.R., Bellwood, D.R., Tornabene, L., 2018. The hidden half: ecology and evolution of cryptobenthic fishes on coral reefs. *Biol. Rev.* 93, 1846–1873. <https://doi.org/10.1111/bvr.12423>.
- Brandl, S.J., Rasher, D.B., Côté, I.M., Casey, J.M., Darling, E.S., Lefcheck, J.S., et al., 2019. Coral reef ecosystem functioning: eight core processes and the role of biodiversity. *Front. Ecol. Environ.* 17, 445–454. <https://doi.org/10.1002/fee.2088>.
- Bright, T., Lang, J., 2013. Picture Guide to Stony Corals of Glovers Reef Atoll. Wildlife Conservation Society, New York.
- Brodie, J., Waterhouse, J., 2012. A critical review of environmental management of the not 'so Great' Barrier Reef. *Estuar. Coast. Shelf Sci.* 104–105, 1–22. <https://doi.org/10.1016/j.ecss.2012.03.012>.
- Cairns, S.D., 2000. A revision of the shallow-water azooxanthellate Scleractinia of the Western Atlantic. *Stud. Nat. Hist. Caribb. Reg.* 75, 1–240.
- Carballo-Bolaños, R., Seemann, J., Gonzalez, C.T., 2012. A field identification guide to hard corals of Bocas del Toro Archipelago, Panama. http://stri-sites.si.edu/sites/taxonomy_training/wp-content/uploads/2019/04/201215_Hard_Coral_Identifier_guide.pdf.
- Cardoso, A.P., Matos, M.R., Rosa, R.S., Alvarado, F., Medeiros, A.P., Santos, B.A., 2020. Increased fish diversity over day and night in structurally complex habitats of artificial reefs. *J. Exp. Mar. Biol. Ecol.* 522, 151244. <https://doi.org/10.1016/j.jembe.2019.151244>.
- Carpenter, K.E., Abrar, M., Aeby, G., Aronson, R.B., Banks, S., Bruckner, A., et al., 2008. One-third of reef-building coral face elevated extinction risk from climate change and local impacts. *Science* 321, 560–563. <https://doi.org/10.1126/science.1159196>.
- Chaput, R., Paris, C.B., Smith, S.G., Baker, A.C., 2019. Reef fish larvae visually discriminate coral diversity during settlement. *Bull. Mar. Sci.* 95, 449–458. <https://doi.org/10.5343/bms.2018.0063>.
- Cinner, J.E., McClanahan, T.R., MacNeil, M., Graham, N.A., Daw, T.M., Mukminin, A., et al., 2012. Comanagement of coral reef social-ecological systems. *Proc. Natl. Acad. Sci. USA* 109, 5219–5222. <https://doi.org/10.1073/pnas.1121215109>.
- Cleary, D.F.R., Becking, L.E., de Voogd, N.J., Renema, W., de Beer, M., van Soest, R.W.M., et al., 2005. Variation in the diversity and composition of benthic taxa as a function of distance offshore, depth and exposure in the Spermonde Archipelago, Indonesia. *Estuar. Coast. Shelf Sci.* 65, 557–570. <https://doi.org/10.1016/j.ecss.2005.06.025>.
- Cleary, D.F.R., Suharsono, Hoeksema, B.W., 2006. Coral diversity across a disturbance gradient in the Pulau Seribu reef complex off Jakarta, Indonesia. *Biodivers. Conserv.* 15, 3653–3674. <https://doi.org/10.1007/s10531-004-4692-y>.
- Collin, R., Díaz, M.C., Norenburg, J.L., Rocha, R.M., Sánchez, J.A., Schulze, A., et al., 2005. Photographic identification guide to some common marine invertebrates of Bocas del Toro, Panama. *Caribb. J. Sci.* 41, 638–707.

- Colwell, R.K., 2010. Estimating species richness. In: Magurran, A.E., McGill, B.J. (Eds.), *Biological Diversity*. Oxford University Press, Oxford, pp. 39–54.
- Colwell, R.K., 2013. EstimateS: statistical estimation of species richness and shared species from samples. User's Guide and application published at: Version 9.1.0. <http://purl.oclc.org/estimates>.
- Colwell, R.K., Mao, C.X., Chang, J., 2004. Interpolating, extrapolating, and comparing incidence-based species accumulation curves. *Ecology* 85, 2717–2727. <https://doi.org/10.1890/03-0557>.
- Core Team, R., 2018. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org>.
- Cortés-Useche, C., Muñoz-Castillo, A.I., Calle-Triviño, J., Yathiraj, R., Arias-González, J. E., 2019. Reef condition and protection of coral diversity and evolutionary history in the marine protected areas of Southeastern Dominican Republic. *Reg. Stud. Mar. Sci.* 32, 100893 <https://doi.org/10.1016/j.rjsma.2019.100893>.
- Davies, M.R., Piontek, S., 2017. The marine fishes of St. Eustatius, Dutch Caribbean. *Mar. Biodivers.* 47, 27–35. <https://doi.org/10.1007/s12526-016-0575-1>.
- de Bakker, D.M., van Duyl, F.C., Perry, C.T., Meesters, E.H., 2019. Extreme spatial heterogeneity in carbonate accretion potential on a Caribbean fringing reef linked to local human disturbance gradients. *Global Change Biol.* 25, 4092–4104. <https://doi.org/10.1111/gcb.14800>.
- De Brauwier, M., Harvey, E.S., McIlwain, J.L., Hobbs, J.P.A., Jompa, J., Burton, M., 2017. The economic contribution of the muck dive industry to tourism in Southeast Asia. *Mar. Pol.* 83, 92–99. <https://doi.org/10.1016/j.marpol.2017.05.033>.
- De Brauwier, M., Harvey, E.S., Ambo-Rappe, R., McIlwain, J.L., Jompa, J., Saunders, B.J., 2019. High diversity, but low abundance of cryptobenthic fishes on soft sediment habitats in Southeast Asia. *Estuar. Coast Shelf Sci.* 217, 110–119. <https://doi.org/10.1016/j.ecss.2018.11.014>.
- de Graaf, M., Piontek, S., Miller, C.M., Brenuel, T., Nagelkerke, L.A.J., 2015. Status and trends of St. Eustatius coral reef ecosystem and fisheries: 2015 report card. *IMARES Report C167/15*, 41.
- De Souza, J.N., Nunes, F.L.D., Zilberberg, C., Sanchez, J.A., Migotto, A.E., Hoeksema, B. W., et al., 2017. Contrasting patterns of connectivity among endemic and widespread fire coral species (*Millepora* spp.) in the tropical Southwestern Atlantic. *Coral Reefs* 36, 701–716. <https://doi.org/10.1007/s00338-017-1562-0>.
- Debrot, A.O., Houtepen, E., Meesters, H.W.G., van Beek, L.J.M., Timmer, T., Boman, E.K., et al., 2014. Habitat Diversity and Biodiversity of the Benthic Seascapes of St. Eustatius, vol. 14. *IMARES Report C078*, p. 43.
- Ditzel, P., König, S., Musembi, P., Peters, M.K., 2022. Correlation between coral reef condition and the diversity and abundance of fishes and sea urchins on an East African coral reef. *Oceans* 3, 1–14. <https://doi.org/10.3390/oceans3010001>.
- Durán-Fuentes, J., Gracia, A., Santodomingo, N., 2021. Occurrence of the azooxanthellate coral *Phyllangia pequegnatae* (Scleractinia: caryophylliidae) in the Colombian Caribbean Sea: hidden diversity or another invasive species? *Mar. Biodivers.* 51, 34. <https://doi.org/10.1007/s12526-021-01175-y>.
- Edgar, G.J., Stuart-Smith, R.D., Willis, T.J., Kininmonth, S., Baker, S.C., Banks, S., et al., 2014. Global conservation outcomes depend on marine protected areas with five key features. *Nature* 506, 216–220. <https://doi.org/10.1038/nature13022>.
- Edinger, E.N., Jompa, J., Limmon, G.V., Widjatmoko, W., Risk, M.J., 1998. Reef degradation and coral biodiversity in Indonesia: effects of land-based pollution, destructive fishing practices and changes over time. *Mar. Pollut. Bull.* 36, 617–630. [https://doi.org/10.1016/S0025-326X\(98\)00047-2](https://doi.org/10.1016/S0025-326X(98)00047-2).
- Emslie, M.J., Logan, M., Williamson, D.H., Ayling, A.M., MacNeil, M., Ceccarelli, D., et al., 2015. Expectations and outcomes of reserve network performance following re-zoning of the Great Barrier Reef Marine Park. *Curr. Biol.* 25, 983–992. <https://doi.org/10.1016/j.cub.2015.01.073>.
- Esteban, N., 2005. St. Eustatius National Parks Foundation: Annual Report 2004. *STENAPA, St. Eustatius*, p. 40.
- Fabinyi, M., 2008. Dive tourism, fishing and marine protected areas in the Calamianes Islands, Philippines. *Mar. Policy* 32, 898–904. <https://doi.org/10.1016/j.marpol.2008.01.004>.
- Fabrizius, K., De'ath, G., 2008. Photosynthetic symbionts and energy supply determine octocoral biodiversity in coral reefs. *Ecology* 89, 3163–3173. <https://doi.org/10.1890/08-0005.1>.
- Fenner, D.P., 1993. Species distinctions among several Caribbean stony corals. *Bull. Mar. Sci.* 53, 1099–1116.
- Fox, J., Weisberg, S., 2011. *An {R} Companion to Applied Regression*, second ed. Sage, Thousand Oaks CA.
- García-Hernández, J.E., van Moorsel, G.W.N.M., Hoeksema, B.W., 2017. Lettuce corals overgrowing tube sponges at St. Eustatius, Dutch Caribbean. *Mar. Biodivers.* 47, 55–56. <https://doi.org/10.1007/s12526-016-0467-4>.
- Giglio, V.J., Ternes, M.L.F., Kassuga, A.D., Ferreira, C.E.L., 2018. Scuba diving and sedentary fish watching: effects of photographer approach on seahorse behavior. *J. Ecotourism* 18, 142–151. <https://doi.org/10.1080/14724049.2018.1490302>.
- Gittenberger, A., Draisma, S.G., Arbi, U.Y., Langenberg, V., Erftemeijer, P.L., Tuti, Y., et al., 2015. Coral reef organisms as bioregion indicators off Halmahera, Moluccas, Indonesia. *Aquat. Conserv. Mar. Freshw. Ecosyst.* 25, 743–755. <https://doi.org/10.1002/aqc.2495>.
- Greenfield, D.W., Johnson, R.K., 1999. Assemblage structure and habitat associations of western Caribbean gobies (Teleostei: gobiidae). *Copeia* 251–266. <https://doi.org/10.2307/1447470>, 1999.
- Guzman, H.M., Guevara, C.A., Breedy, O., 2004. Distribution, diversity, and conservation of coral reefs and coral communities in the largest marine protected area of the Pacific Panama (Coiba Island). *Environ. Conserv.* 31, 111–121. <https://doi.org/10.1017/S0376892904001250>.
- Hackradt, C.W., Félix-Hackradt, F.C., García-Charton, J.A., 2011. Influence of habitat structure on fish assemblage of an artificial reef in southern Brazil. *Mar. Environ. Res.* 72, 235–247. <https://doi.org/10.1016/j.marenvres.2011.09.006>.
- Harborne, A.R., Jelks, H.L., Smith-Vaniz, W.F., Rocha, L.A., 2012. Abiotic and biotic controls of cryptobenthic fish assemblages across a Caribbean seascape. *Coral Reefs* 31, 977–990. <https://doi.org/10.1007/s00338-012-0938-4>.
- Heery, E.C., Hoeksema, B.W., Browne, N.K., Reimer, J.D., Ang, P.O., Huang, D., et al., 2018. Urban coral reefs: degradation and resilience of hard coral assemblages in coastal cities of East and Southeast Asia. *Mar. Pollut. Bull.* 135, 654–681. <https://doi.org/10.1016/j.marpolbul.2018.07.041>.
- Hill, C.E.L., Lympiraki, M.M., Hoeksema, B.W., 2021. A centuries-old manmade reef in the Caribbean does not substitute natural reefs in terms of species assemblages and interspecific competition. *Mar. Pollut. Bull.* 169, 112576. <https://doi.org/10.1016/j.marpolbul.2021.112576>.
- Hoeksema, B.W., 2007. Delineation of the Indo-Malayan centre of maximum marine biodiversity: the Coral Triangle. In: Renema, W. (Ed.), *Biogeography, Time, and Place: Distributions, Barriers, and Islands*. Springer, The Netherlands, pp. 117–178. https://doi.org/10.1007/978-1-4020-6374-9_5.
- Hoeksema, B.W., 2015. Latitudinal species diversity gradient of mushroom corals off eastern Australia: a baseline from the 1970s. *Estuar. Coast Shelf Sci.* 165, 190–198. <https://doi.org/10.1016/j.ecss.2015.05.015>.
- Hoeksema, B.W., 2016. *Naturalis Biodiversity Center, Leiden. Marine biodiversity survey of St. Eustatius, Dutch Caribbean, 2015. and ANEMOON Foundation, Bennebroek, The Netherlands*, p. 157.
- Hoeksema, B.W., Cairns, S., 2021. World List of Scleractinia. Accessed at: <http://www.marinespecies.org/scleractinia> on 2021-12-01.
- Hoeksema, B.W., Giyanto, Suharsono, 2019a. The role of maximum shelf depth versus distance from shore in explaining a diversity gradient of mushroom corals (Fungiidae) off Jakarta. *Diversity* 11, 46. <https://doi.org/10.3390/d11030046>.
- Hoeksema, B.W., Hiemstra, A.F., Vermeij, M.J.A., 2019b. The rise of a native sun coral species on southern Caribbean coral reefs. *Ecosphere* 10, e02942. <https://doi.org/10.1002/ecs2.2942>.
- Hoeksema, B.W., Koh, E.G.L., 2009. Depauperation of the mushroom coral fauna (Fungiidae) of Singapore (1860s–2006) in changing reef conditions. *Raffles Bull. Zool. Suppl.* 22, 91–101.
- Hoeksema, B.W., Smith-Moorhouse, A., Harper, C.E., van der Schoot, R.J., Timmerman, R.F., Spaargaren, R., Langdon-Down, S.J., 2022c. Black mantle tissue of endolithic mussels (*Leiosolenus* spp.) is cloaking borehole orifices in Caribbean reef corals. *Diversity* 14 (5), 401. <https://doi.org/10.3390/d14050401>.
- Hoeksema, B.W., ten Hove, H.A., 2017. Attack on a Christmas tree worm by a Caribbean sharpnose pufferfish at St. Eustatius, Dutch Caribbean. *Bull. Mar. Sci.* 93, 1023–1024. <https://doi.org/10.5343/bms.2017.1059>.
- Hoeksema, B.W., van der Meij, S.E.T., Franssen, C.H.J.M., 2012. The mushroom coral as a habitat. *J. Mar. Biol. Assoc. U. K.* 92, 647–663. <https://doi.org/10.1017/S0025315411001445>.
- Hoeksema, B.W., Reimer, J.D., Vonk, R., 2017a. Editorial: biodiversity of Caribbean coral reefs (with a focus on the Dutch Caribbean). *Mar. Biodivers.* 47, 1–10. <https://doi.org/10.1007/s12526-017-0641-3>.
- Hoeksema, B.W., van Beusekom, M., ten Hove, H.A., Ivanenko, V.N., van der Meij, S.E.T., van Moorsel, G.W.N.M., 2017b. *Helioseris cucullata* as a host coral at St. Eustatius, Dutch Caribbean. *Mar. Biodivers.* 47, 71–78. <https://doi.org/10.1007/s12526-016-0599-6>.
- Hoeksema, B.W., Hassell, D., Meesters, E.H.W.G., van Duyl, F.C., 2018. Wave-swept coralliths of Saba Bank, Dutch Caribbean. *Mar. Biodivers.* 48, 2003–2016. <https://doi.org/10.1007/s12526-017-0712-5>.
- Hoeksema, B.W., García-Hernández, J.E., van Moorsel, G.W.N.M., Olthoff, G., ten Hove, H.A., 2020. Extension of the recorded host range of Caribbean Christmas tree worms (*Spirobranchus* spp.) with two scleractinians, a zoantharian, and an ascidian. *Diversity* 12, 115. <https://doi.org/10.3390/d12030115>.
- Hoeksema, B.W., Harper, C.E., Langdon-Down, S.J., van der Schoot, R.J., Smith-Moorhouse, A., Spaargaren, R., Timmerman, R.F., 2022a. Host range of the coral-associated worm snail *Petalocochus* sp. (Gastropoda: vermetidae), a newly discovered cryptogenic pest species in the Southern Caribbean. *Diversity* 14, 196. <https://doi.org/10.3390/d14030196>.
- Hoeksema, B.W., Timmerman, R.F., Spaargaren, R., Smith-Moorhouse, A., van der Schoot, R.J., Langdon-Down, S.J., Harper, C.E., 2022b. Morphological modifications and injuries of corals caused by symbiotic feather duster worms (Sabellidae) in the Caribbean. *Diversity* 14, 332. <https://doi.org/10.3390/d14050332>.
- Homes, W., 2021. *Quantifying the State of the Coral Reef Ecosystem in Relation to Biophysical Benthic and Pelagic Indicators and Biological Drivers of Change in the Saba National Marine Park, Dutch Caribbean*. MSc thesis. Swedish University of Agricultural Sciences, Uppsala, p. 100.
- Howell, K.L., Holt, R., Endrino, I.P., Stewart, H., 2011. When the species is also a habitat: comparing the predictively modelled distributions of *Lophelia pertusa* and the reef habitat it forms. *Biol. Conserv.* 144, 2656–2665. <https://doi.org/10.1016/j.biocon.2011.07.025>.
- Huang, D., Hoeksema, B.W., Affendi, Y.A., Ang, P.O., Chen, C.A., Huang, H., et al., 2016. Conservation of reef corals in the South China Sea based on species and evolutionary diversity. *Biodivers. Conserv.* 25, 331–344. <https://doi.org/10.1007/s10531-016-1052-7>.
- Hughes, T.P., Tanner, J.E., 2000. Recruitment failure, life histories, and longterm decline of Caribbean corals. *Ecology* 81, 2250–2263. <https://doi.org/10.2307/177112>.
- Hughes, T.P., Barnes, M.L., Bellwood, D.R., Cinner, J.E., Cumming, G.S., Jackson, J.B.C., et al., 2017. Coral reefs in the anthropocene. *Nature* 546, 82–90. <https://doi.org/10.1038/nature22901>.

- Hughes, T.P., Anderson, K.D., Connolly, S.R., Heron, S.F., Kerry, J.T., Lough, J.M., et al., 2018. Spatial and temporal patterns of mass bleaching of corals in the Anthropocene. *Science* 359, 80–83. <https://doi.org/10.1126/science.aan8048>.
- Humann, P., DeLoach, N., 2013. Reef Coral Identification: Florida, Caribbean, Bahamas, third ed. New World Publications, Jacksonville.
- Huston, M.A., 1985. Patterns of species diversity on coral reefs. *Annu. Rev. Ecol. Systemat.* 16, 149–177. <https://doi.org/10.1146/annurev.es.16.110185.001053>.
- Hylkema, A., Debrot, A.O., Osinga, R., Bron, P.S., Heesink, D.B., Izioka, A.K., et al., 2020. Fish assemblages of three common artificial reef designs during early colonization. *Ecol. Eng.* 157, 105994 <https://doi.org/10.1016/j.ecoeng.2020.105994>.
- Japaud, A., Fauvelot, C., Bouchon, C., 2014. Unexpected high densities of the hybrid coral *Acropora prolifera* (Lamarck 1816) in Guadeloupe island, lesser Antilles. *Coral Reefs* 33, 593. <https://doi.org/10.1007/s00338-014-1169-7>.
- Kitahara, M.V., Fukami, H., Benzoni, F., Huang, D., 2016. The new systematics of Scleractinia: integrating molecular and morphological evidence. In: Goffredo, S., Dubinsky, Z. (Eds.), *The Cnidaria, Past, Present and Future*. Springer, Switzerland, pp. 41–59. https://doi.org/10.1007/978-3-319-31305-4_4.
- Kitson-Walters, K., 2017. St. Eustatius GCRMN Caribbean Final Report 2017. Caribbean Netherlands Science Institute, St. Eustatius, p. 22.
- Komyakova, V., Munday, P.L., Jones, G.P., 2013. Relative importance of coral cover, habitat complexity and diversity in determining the structure of reef fish communities. *PLoS One* 8, e83178. <https://doi.org/10.1371/journal.pone.0083178>.
- Legendre, P., Legendre, L., 2012. Ordination in reduced space. *Dev. Environ. Model.* 24, 425–520. <https://doi.org/10.1016/B978-0-444-53868-0.50009-5>.
- Lymperaki, M.M., Hill, C.E.L., Hoeksema, B.W., 2022. The effects of wave exposure and host cover on coral-associated fauna of a centuries-old artificial reef in the Caribbean. *Ecol. Eng.* 176, 106536 <https://doi.org/10.1016/j.ecoeng.2021.106536>.
- MacRae, D.R., Esteban, N., 2007. St. Eustatius Marine Park Management Plan 2007. Coastal Zone Management (UK) and St. Eustatius National Parks Foundation. (STENAPA), St. Eustatius, p. 126.
- Maggioli, D., Arrigoni, R., Seveso, D., Galli, P., Berumen, M.L., Denis, V.L., et al., 2022. Evolution and biogeography of the *Zanclus*-Scleractinia symbiosis. *Coral Reefs* 41, 779–795. <https://doi.org/10.1007/s00338-020-02010-9>.
- McClellan, K., 2009. Evaluating the Effectiveness of Marine No-Take Reserves in St. Eustatius, Netherlands Antilles. MSc thesis, Duke University, Durham, North Carolina, p. 67.
- McKenna, S.A., Etnoyer, P., 2010. Rapid assessment of stony coral richness and condition on Saba Bank, Netherlands Antilles. *PLoS One* 5, e10749. <https://doi.org/10.1371/journal.pone.0010749>.
- Meesters, E.H., Mueller, B., Nugues, M.M., 2013. Caribbean free-living coral species co-occurring deep off the windward coast of Curaçao. *Coral Reefs* 32, 109. <https://doi.org/10.1007/s00338-012-0960-6>.
- Mellin, C., MacNeil, M.A., Cheal, A.J., Emslie, M.J., Caley, M.J., 2016. Marine protected areas increase resilience among coral reef communities. *Ecol. Lett.* 19, 629–637. <https://doi.org/10.1111/ele.12598>.
- Miller, M., Williams, D.E., Huntington, B.E., Piniak, G.A., Vermeij, M.J.A., 2016. Decadal comparison of a diminishing coral community: a study using demographics to advance inferences of community status. *PeerJ* 4, e1643. <https://doi.org/10.7717/peerj.1643>.
- Miller, I., Cheal, A.J., Emslie, M.J., Logan, M., Sweatman, H., 2012. Ongoing effects of no-take marine reserves on commercially exploited coral trout population on the Great Barrier Reef. *Mar. Environ. Res.* 79, 167–170. <https://doi.org/10.1016/j.marenvres.2012.05.008>.
- Montano, S., 2020. The extraordinary importance of coral-associated fauna. *Diversity* 12, 357. <https://doi.org/10.3390/D12090357>.
- Mora, C., Andrefouët, S., Costello, M.J., Kranenburg, C., Rollo, A., Veron, J., et al., 2006. Coral reefs and the global network of marine protected areas. *Science* 312, 1750–1751. <https://doi.org/10.1126/science.1125295>.
- Morzaria-Luna, H., Cruz-Piñón, G., Brusca, R.C., López-Ortiz, A.M., Moreno-Báez, M., Reyes-Bonilla, H., et al., 2018. Biodiversity hotspots are not congruent with conservation areas in the Gulf of California. *Biodivers. Conserv.* 14, 3819–3842. <https://doi.org/10.1007/s10531-018-1631-x>.
- Muir, P.R., Obura, D.O., Hoeksema, B.W., Sheppard, C., Pichon, M., Richards, Z.T., 2022. Conclusions of low extinction risk for most species of reef-building corals are premature. *Nature Ecol. Evol.* 6, 357–358. <https://doi.org/10.1038/s41559-022-01659-5>.
- Mumby, P.J., Harborne, A.R., 2010. Marine reserves enhance the recovery of corals on Caribbean reefs. *PLoS One* 5, e8657. <https://doi.org/10.1371/journal.pone.0008657>.
- Neves, E., Johnsson, R., Sampaio, C., Pichon, M., 2006. The occurrence of *Scolymia cubensis* in Brazil: revising the problem of the Caribbean solitary mussids. *Zootaxa* 1366, 45–54. <https://doi.org/10.11646/ZOOTAXA.1366.1.2>.
- Nunes, F., Fukami, H., Vollmer, S.V., Knowlton, N., 2008. Re-evaluation of the systematics of the endemic corals of Brazil by molecular data. *Coral Reefs* 27, 423–432. <https://doi.org/10.1007/s00338-007-0349-0>.
- Öhman, M.C., Rajasuriya, A., 1998. Relationships between habitat structure and fish communities on coral. *Environ. Biol. Fish.* 53, 19–31. <https://doi.org/10.1023/A:1007445226928>.
- Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., et al., 2016. Vegan: community ecology package. R package version 2.3-4. <http://CRAN.R-project.org/package=vegan>.
- Ortiz Cajica, A.K., Hinojosa-Arango, G., Garza-Pérez, J.R., Rioja-Nieto, R., 2020. Seascape metrics, spatio-temporal change, and intensity of use for the spatial conservation prioritization of a Caribbean marine protected area. *Ocean Coast. Manag.* 194, 105265 <https://doi.org/10.1016/j.ocecoaman.2020.105265>.
- Patton, W.K., 1976. Animal associates of living reef corals. In: Jones, O.A., Endean, R. (Eds.), *Biology and Geology of Coral Reefs*. Biol. 2, vol. 3. Academic Press, New York, pp. 1–36.
- Petrosillo, I., Zurlini, G., Corliano, M.E., Zaccarelli, N., Dadamo, M., 2007. Tourist perception of recreational environment and management in a marine protected area. *Landsc. Urban Plann.* 79, 29–37. <https://doi.org/10.1016/j.landurbplan.2006.02.017>.
- Plaisance, L., Caley, M.J., Brainard, R.E., Knowlton, N., 2011. The diversity of coral reefs: what are we missing? *PLoS One* 6, e25026. <https://doi.org/10.1371/journal.pone.0025026>.
- Prada, C., DeBiase, M.B., Neigel, J.E., Yednock, B., Stake, J.L., Forsman, Z.H., et al., 2014. Genetic species delineation among branching Caribbean *Porites* corals. *Coral Reefs* 33, 1019–1030. <https://doi.org/10.1007/s00338-014-1179-5>.
- Pressey, R.L., Visconti, P., Ferraro, P.J., 2015. Making parks make a difference: poor alignment of policy, planning and management with protected-area impact, and ways forward. *Phil. Trans. R. Soc. B* 370, 20140280 <https://doi.org/10.1098/rstb.2014.0280>.
- Rees, M.J., Knott, N.A., Neilson, J., Linklater, M., Osterloh, I., Jordan, A., et al., 2018. Accounting for habitat structural complexity improves the assessment of performance in no-take marine reserves. *Biol. Conserv.* 224, 100–110. <https://doi.org/10.1016/j.biocon.2018.04.040>.
- Reyes, J., Santodomingo, N., Flórez, P., 2010. Corales Escleractinios de Colombia. Instituto de Investigaciones Marinas y Costeras (INVEMAR), Santa Marta, Colombia., pp. 1–246.
- Richardson, L.E., Graham, N.A.J., Hoey, A.S., 2017. Cross-scale habitat structure driven by coral species composition on tropical reefs. *Sci. Rep.* 7, 7557. <https://doi.org/10.1038/s41598-017-08109-4>.
- Roberts, C., 2012. Marine ecology: reserves do have key role in fisheries. *Curr. Biol.* 22, R444–R446. <https://doi.org/10.1016/j.cub.2012.04.030>.
- Roberts, T.E., Bridge, T.C.L., Caley, M.J., Madin, J.S., Baird, A.H., 2019. Resolving the depth zonation paradox in reef corals. *Ecology* 100, e02761. <https://doi.org/10.1002/ecy.2761>.
- Robertson, D.R., Estape, C.J., Estape, A.M., Pena, E., Tornabene, L., Baldwin, C.C., 2020. The marine fishes of St. Eustatius Island, northeastern Caribbean: an annotated, photographic catalog. *ZooKeys* 1007, 145–180. <https://doi.org/10.3897/zookeys.1007.58515>.
- Roos, P.J., 1971. The shallow-water corals of The Netherlands Antilles. *Stud. Fauna Curaçao Caribb. Isl.* 130, 1–50.
- Rudd, M.A., Tupper, M.H., 2002. The impact of Nassau grouper size and abundance on SCUBA diver site selection and MPA economics. *Coast. Manag.* 30, 133–151. <https://doi.org/10.1080/089207502753504670>.
- Santodomingo, N., Reyes, J., Flórez, P., Chacón-Gómez, I.C., van Ofwegen, L.P., Hoeksema, B.W., 2013. Diversity and distribution of azooxanthellate corals in the Colombian Caribbean. *Mar. Biodivers.* 43, 7–22. <https://doi.org/10.1007/s12526-012-0131-6>.
- Scott, P.J.B., 1987. Associations between corals and macro-infaunal invertebrates in Jamaica, with a list of Caribbean and Atlantic coral associates. *Bull. Mar. Sci.* 40, 271–286.
- Selig, E.R., Bruno, J.F., 2010. A global analysis of the effectiveness of marine protected areas in preventing coral loss. *PLoS One* 5, e9278. <https://doi.org/10.1371/journal.pone.0009278>.
- Slijkerman, D.M.E., Meesters, E.H., Becking, L.E., 2016. Marine Assessment Guidelines for BOPEC and NUSTAR Operations, vol. 16. IMARES Report C056/, p. 27.
- Smith, J., 2008. In-water Monitoring of Sea Turtle Aggregations in St. Eustatius National Marine Park. Eustatius National Parks Foundation, Oranjestad, p. 20.
- Spash, C.L., 2000. Assessing the benefits of improving coral reef biodiversity: the contingent valuation method. In: Cesar, H.S.J. (Ed.), *Collected Essays on the Economics of Coral Reefs*. Cordio, Kalmar Sweden, pp. 40–54.
- Stella, J.S., Pratchett, M.S., Hutchings, P.A., Jones, G.P., 2011. Coral-associated invertebrates: diversity, ecology importance and vulnerability to disturbance. *Oceanogr. Mar. Biol. Annu. Rev.* 49, 43–104. <https://doi.org/10.1201/b11009-3>.
- Sybesma, J., van 't Hof, T., Pors, L.P.J.J., 1993. Marine Area Survey – an Inventory of the Natural and Cultural Marine Resources of St. Eustatius, Netherlands Antilles. CARMABI, Curaçao, p. 73.
- Thur, S.M., 2010. User fees as sustainable financing mechanisms for marine protected areas: an application to the Bonaire National Marine Park. *Mar. Policy* 34, 63–69. <https://doi.org/10.1016/j.marpol.2009.04.008>.
- Tieskens, K., Schep, S., van Beukering, P., van Beek, I., Wolfs, E., 2014. Mapping the Economic Value of Ecosystems on St. Eustatius. IVM Institute for Environmental Studies, VU University Amsterdam, p. 36. <https://www.dcbd.nl/sites/default/files/documents/R14-13-Value-mapping-of-nature-on-St-Eustatius.pdf>.
- Tornabene, L., Ahmadi, G.N., Berumen, M.L., Smith, D.J., Jompa, J., Pezold, F., 2013. Evolution of microhabitat association and morphology in a diverse group of cryptobenthic coral reef fishes (Teleostei: Gobiidae: *Eviota*). *Mol. Phylogenet. Evol.* 66, 391–400. <https://doi.org/10.1016/j.ympev.2012.10.014>.
- Uyarrá, M.C., Côté, I.M., 2007. The quest for cryptic creatures: impacts of species-focused recreational diving on corals. *Biol. Conserv.* 136, 77–84. <https://doi.org/10.1016/j.biocon.2006.11.006>.
- van Beek, I.J.M., Meesters, E.H.W.G., 2013. Saba Bank Research Expedition 2011 - Progress Report. IMARES Wageningen UR, Wageningen, p. 46. Report C018/13.
- van Beek, I.J.M., Meesters, E.H.W.G., 2014. Saba Bank Research Expedition 2013 - Progress Report. IMARES Wageningen UR, Wageningen, p. 45. Report C086/14.
- van der Land, J., 1977. The Saba Bank—a large atoll in the northeastern Caribbean. *FAO Fish. Rep.* 200, 469–481.
- van der Loos, L.M., Prud'homme van Reine, W.F., Stokvis, F.R., Speksnijder, A.G.C.L., Hoeksema, B.W., 2017. Beta diversity of macroalgal communities around St.

- Eustatius, Dutch Caribbean. *Mar. Biodivers.* 47, 123–138. <https://doi.org/10.1007/s12526-016-0608-9>.
- van der Meij, S.E.T., Suharsono, Hoeksema, B.W., 2010. Long-term changes in coral assemblages under natural and anthropogenic stress in Jakarta Bay (1920–2005). *Mar. Pollut. Bull.* 60, 1442–1454. <https://doi.org/10.1016/j.marpolbul.2010.05.011>.
- van Kuijk, T., de Graaf, M., Nagelkerke, L., Boman, E., Debrot, A.O., 2015. Baseline Assessment of the Coral Fish Assemblages of St. Eustatius, vol. 15. IMARES Report C058/, p. 51.
- Vermeij, M.J.A., Bakker, J., van der Hal, N., Bak, R.P.M., 2011. Juvenile coral abundance has decreased by more than 50% in only three decades on a small Caribbean island. *Diversity* 3, 296–307. <https://doi.org/10.3390/d3030296>.
- Vianna, G.M., Meekan, M.G., Rogers, A.A., Kragt, M.E., Alin, J.M., Zimmerhackel, J.S., 2018. Shark-diving tourism as a financing mechanism for shark conservation strategies in Malaysia. *Mar. Policy* 94, 220–226. <https://doi.org/10.1016/j.marpol.2018.05.008>.
- Waheed, Z., Hoeksema, B.W., 2013. A tale of two winds: species richness patterns of reef corals around the Semporna peninsula, Malaysia. *Mar. Biodivers.* 43, 37–51. <https://doi.org/10.1007/s12526-012-0130-7>.
- Waheed, Z., Hoeksema, B.W., 2014. Diversity patterns of Scleractinian corals at Kota Kinabalu, Malaysia, in relation to exposure and depth. *Raffles Bull. Zool.* 62, 66–82.
- Waheed, Z., van Mil, H.G.J., Syed Hussein, M.A., Jumin, R., Golom Ahad, B., Hoeksema, B.W., 2015. Coral reefs at the northernmost tip of Borneo: An assessment of scleractinian species richness patterns and benthic reef assemblages. *PLoS One* 10, e0146006. <https://doi.org/10.1371/journal.pone.0146006>.
- Ward, J.R., Rypien, K.L., Bruno, J.F., Harvell, C.D., Jordán-Dahlgren, E., Mullen, K.M., et al., 2006. Coral diversity and disease in Mexico. *Dis. Aquat. Org.* 69, 23–31. <https://doi.org/10.3354/dao069023>.
- Weible, R.M., Rodgers, K.S., Friedlander, A.M., Hunter, C.L., 2021. Assessing assemblage composition of reproductively mature resource fishes at a community based subsistence fishing area (CBSFA). *Diversity* 13, 114. <https://doi.org/10.3390/d13030114>.
- White, J., Esteban, N., Polino, M., 2006. Fisheries Baseline Assessment of Statia Marine Park, St Eustatius, Netherlands Antilles. St Eustatius National Parks Foundation, St Eustatius, p. 31.
- White, J., Esteban, N., MacRae, D., 2007. St. Eustatius Marine Park Tanker Anchoring Impact Study and Recommendations. St Eustatius National Parks Foundation, St Eustatius, p. 29.
- Wilson, S.K., Fisher, R., Pratchett, M., 2013. Differential use of shelter holes by sympatric species of blennies (Blenniidae). *Mar. Biol.* 160, 2405–2411. <https://doi.org/10.1007/s00227-013-2235-3>.
- Wright, L.S., 2022. Small no-take areas benefit hard corals more than regulation through fishing permits. *Aquat. Conserv. Mar. Freshw. Ecosyst.* <https://doi.org/10.1002/aqc.3814>.
- Yusuf, S., Beger, M., Tassakka, A.C.M.A.R., De Brauwier, M., Pricella, A., Rahmi Umar, W., et al., 2021. Cross shelf gradients of scleractinian corals in the spermonde islands, south sulawesi, Indonesia. *Biodiversitas* 22, 1415–1423. <https://doi.org/10.13057/biodiv/d220344>.
- Zhao, Q., Stephenson, F., Lundquist, C., Kaschner, K., Jayathilake, D., Costello, M.J., 2020. Where Marine Protected Areas would best represent 30% of ocean biodiversity. *Biol. Conserv.* 244, 108536 <https://doi.org/10.1016/j.biocon.2020.108536>.
- Zlatarski, V.N., Estalella, N.M., 1982. Les Scléactiniaires de Cuba avec des données sur les organismes associés. Editions de l'Académie Bulgare des Sciences, Sofia.
- Zlatarski, V.N., Greenstein, B.J., 2020. The reticulate coral reef system in Golfo de Guacanayabo, SE Cuba. *Coral Reefs* 39, 509–513. <https://doi.org/10.1007/s00338-020-01933-7>.