Impacts of environmental changes on the global distribution of coral reefs

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Abstract

Coral reefs support high biological diversity of marine life, and are highly productive ecosystems. They are of substantial social, cultural, and economic importance. Coral reefs typically exist in warm and clear shallow ocean waters. Their distributions are limited by environmental factors, including temperature, salinity, light, nutrient, and aragonite saturation state. Environmental perturbations exert profound influence on coral reef distribution and reef habitat suitability. Coral reefs are particularly vulnerable to rising seawater temperature as a result of climate change because they already live near their thermal limits. High temperature breaks down the symbiotic relationship between coral host and the endosymbiotic dinoflagellate algae (zooxanthellae), a phenomenon known as coral bleaching. Ocean acidification limits coral growth by reducing the concentration of carbonate ions, which corals need to construct their skeletons, and by simultaneously increasing rates of bioerosion and dissolution on coral reefs, resulting in a shift from net accretion to net dissolution. Other factors such as eutrophication cause negative impacts on coral reefs via directly changing coral growth and calcification and indirectly by stimulating growth of macroalgal, which compete with corals for space and light. Elucidating environmental limits for coral growth and understanding the response of reef habitat suitability to environmental change are hence central to projecting future impacts of climate change on coral reef ecosystems and their biogeography under changing environmental conditions.

This thesis describes and discusses current and future reef habitat suitability and potential reef habitat distribution. First, I use the diagnostic model ReefHab in combination with most recent environmental variables to define the coral reef tolerance limits. The results show that the global, annual averaged tolerance limits are 21.7-29.6°C for sea surface temperature, 28.7-40.4 psu for sea surface salinity, 4.51 μmol L⁻¹ for nitrate, 0.63 μmol L⁻¹ for phosphate, and 2.82 for aragonite saturation state. The averaged minimum light intensity for coral reefs is 450 μmol photons m⁻² s⁻¹. When ReefHab is run with these newly derived tolerance limits, a more accurate potential reef habitat distribution is obtained than with the original tolerance limits.

Second, by using the global data of coral reef occurrence as a proxy for their long-term adaptation to contextual environmental conditions, I calculate the global and regional reef habitat suitability functions. This thesis is focused on six regions: Southeast Asia, Great Barrier Reef (GBR), Great Caribbean Region, Red
Sea and Persian Gulf, Western Indian Ocean, and Central Pacific. Taking regional adaption into account, the results suggest that temporary refugia account for 3% of the reefs in the six regions with respect to variations of +0.1°C in SST, -0.02 in \( \Omega_{a_{w}} \), +0.02 \( \mu \)mol L\(^{-1} \) in NO\(_{3}\), and +0.01 \( \mu \)mol L\(^{-1} \) in PO\(_{4}\). Temporary refugia are areas with increased suitability with respect to all four environmental changes. They are in the Nansha Islands, the Andaman and Nicobar Islands, the Northern Red Sea, and the Turks and Caicos Islands. In contrast, 54% of the reefs in the six regions will face a decrease in habitat suitability with both global (warming and ocean acidification) and local threats (elevated nutrient concentration). These areas are Southeast Asia, the Great Caribbean, Western Indian Ocean, and the central Pacific. Local threats, such as nutrient eutrophication, will affect the central and southern GBR, Persian Gulf, coast of Oman, Kenya, Tanzania, and islands of the Central Pacific (along 20°S), accounting for 26% of the reefs in the six regions. Local conservation managements can potentially increase areas classifiable as temporary refugia by protecting coral reefs from further deterioration, thus buying humanity additional time for producing solutions against global threats. About 17% of the reefs in the six regions will be under global threats, mainly in the Philippines, northern GBR, and New Caledonia.

Third, I explore the impact of global warming and ocean acidification on the potential reef habitat and habitat suitability by applying the tolerance limits and the global reef habitat suitability function in combination with ensemble data of IPCC AR5 climate models using new Representative Concentration Pathway experiments (RCP8.5). The results indicate that the poleward expansion of potential reef habitats due to warming will be limited by ocean acidification eventually. The area of potential reef habitats will decline to half of its 2010 area in 2050. The Great Barrier Reef, the Great Caribbean Region, and high latitude reef locations including Japan, Hawaii, the northern Red Sea, Persian Gulf, southern Madagascar, and Mauritius could serve as temporary refugia under ocean warming. However, by the year 2100, ocean acidification will restrict reef accretion and result in no suitable reef habitat.

I also explore the combined effects of pairwise combinations of environmental factors on coral reefs. The results suggest that temperature and salinity, temperature and phosphate, temperature and aragonite saturation state, salinity and aragonite saturation state, phosphate and aragonite saturation state affect corals non-linearly and in ways that cannot be described by an additive approach. In contrast, the combined effects of changing nitrate with other factors (i.e. temperature, salinity, phosphate, aragonite saturation state) and salinity with phosphate are cumulative and can be described by additive models. This thesis contributes to knowledge on the tolerance limits for coral reefs and the
parametric function of reef habitat suitability. The potential interactions between environmental factors are also preliminarily investigated.
Zusammenfassung


Der Kern dieser Arbeit beschreibt und diskutiert die aktuelle und zukünftige Habitatsignung für Korallen sowie potenzieller Rifflebensräume. Zuerst benutze ich das Diagnosemodell ReefHab in Kombination mit den aktuellsten Werten verschiedener Umweltfaktoren, um entsprechende Toleranzgrenzen zu definieren. Die Ergebnisse zeigen deutlich, dass der globale Jahresdurchschnitt für die Meeresoberflächentemperatur bei 21,7-29,6°C, für den Salzgehalt der Meeresoberfläche bei 28,7-40,4 psu, für Nitrat bei 4,51 µmol L⁻¹, für Phoshpat bei 0,63 µmol L⁻¹ und für den Aragonitsättigungszustand bei 2,82 liegt. Die durchschnittliche minimale Lichtintensität in Korallenriffen beträgt 450 µmol Photonen m⁻² s⁻¹. Das ReefHab-Modell mit diesen neu definierten Toleranzgrenzen liefert eine genauere Beschreibung potenzieller Rifflebensräume als mit den ursprünglichen Toleranzgrenzen.

2100 wird jedoch die Versauerung der Meere die Riffbildung einschränken und zu keinem geeignetem Riffhabitat führen.

Dedication

To my grandparents,
who were with me every step believing in me
I miss you everyday

献给我亲爱的爷爷奶奶

“往而不可追者，年也；去而不可见者，亲也”。

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Declaration on the contribution to multi-author sections

Article 1
Title: Suitable environmental ranges for potential Coral reef habitats in the tropical ocean
Authors: Yi Guan, Sönke Hohn, Agostino Merico
Agostino Merico and Sönke Hohn conceived the idea of the study. I coded the model from scratch and did the analysis and prepared all the results. I wrote the manuscript with help of coauthors.

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Agostino Merico and Sönke Hohn conceived the idea of the study. I did the data analysis and prepared all the results. I wrote the manuscript with help of coauthors.

Article 3
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I conceived the idea of the study. I did the data analysis and prepared all the results. I wrote the manuscript with help of coauthors.

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1 General Introduction

1.1 Coral reefs – values and threats

Corals are marine invertebrate animals within the phylum Cnidaria and the class Anthozoa. Corals can exist as individual polyp, or in large colonies of many polyps. Coral are generally classified as hermatypic coral (hereafter coral) and ahermatypic coral. Photosynthetic dinoflagellate microalgae of the genus *Symbiodinium*, commonly referred to as zooxanthellae, reside in the oral endoderm layer of coral tissue. Corals provide the zooxanthellae with a protected space as well as supply of metabolic by-products (Muscatine and D’elia 1978; Rahav et al. 1989). In addition, corals supply carbon dioxide for zooxanthellae photosynthesis via respiration (Muscatine et al. 1989) and active carbon concentrating mechanisms (CCMs) (Furla et al. 2000; Barott et al. 2015). In exchange, the zooxanthellae provide coral hosts with photosynthetically fixed carbon (e.g. glucose and glycerol), oxygen, and other compounds, including amino acid alanine and organic acids (Davy et al. 2012) that are for corals’ metabolic needs. This coral-dinoflagellate symbiosis makes corals thrive in the oligotrophic waters of the tropics and underpins the growth and formation of coral reefs.

Coral reefs comprise millions of tiny polyps that form large carbonate structures. These biogenic, three-dimensional marine habitats are among the most productive and diverse ecosystems on Earth and have enormous ecological, social, and economic importance (Moberg & Folke 1999; Cesar & Chong 2004). They support almost one third of the world’s marine fish species (Newton et al. 2007) and provide around 10% of the total fish consumed by humans (Pauly et al. 2002). The annual net benefits of healthy coral reefs with tourism potential is estimated between 23,100 and 270,000 US $/m² (Burke et al. 2002). Reefs also play an important role in protecting shorelines from waves, storms, and floods (Ferrario et al. 2014). About 850 million people live within 100 kilometres of coral reefs (Burke et al. 2011) and 100 million or more people benefit from reefs’ production and protection (Ferrario et al. 2014).

However, coral reefs and the ecological benefits they provide are being degraded worldwide (Hughes 1994; Gardner et al. 2003; Pandolfi et al. 2003; Côté et al. 2005; Bruno and Selig 2007; De’ath et al. 2012). In Jamaica, for example, coral abundance has declined from more than 50% in 1970s to less than 5% in 1990s (Hughes 1994). Indo-Pacific coral cover has declined from 42.5% in 1980s to
22.1% by the year 2003 (Bruno and Selig 2007). Coral cover in the Great Barrier Reef showed a decline from 28.0% to 13.8% between 1985 and 2012 (De’ath et al. 2012). In some locations of the Caribbean, especially Curacao, Bonaire, and Belize, and near the Seychelles in the Western Indian Ocean, coral reef ecosystems have already experienced severe phase shifts (McClanahan and Muthiga 1998; Graham et al. 2015; de Bakker et al. 2017). Major causes for reef degradation are high temperature, nutrient enrichments, storms, coastal development, pollution, sedimentation, overfishing, destructive fishing, diseases, and certain local scale anthropogenic activities including coastal construction, coral mining for construction materials (Riegl and Velimirov 1991; Hughes 1994; Mcmanus et al. 1997; Edinger et al. 1998; Al-Jufaili et al. 1999; Aronson and Pretch 2001; Burke et al. 2002; Selig et al. 2006; Bruno and Selig 2007; Bruno et al. 2007; Donner et al. 2007; Hughes et al. 2007; Salm 2010; Eakin et al. 2010; Maynard et al. 2011; Teneva et al. 2012; Randall et al. 2014; Randall and van Woesik 2015). Additionally, the effects of anthropogenic carbon dioxide emissions, such as ocean acidification and rising sea levels, pose a variety of risks to an already threatened ecosystem (Gattuso et al. 1998; Kleypas et al. 1999a; Feely et al. 2004; Hoegh-Guldberg et al. 2007). Hence, it is of utmost importance to understand how environmental conditions limit coral reef distributions and how the coral reef habitat suitability will change with changing environmental conditions, and thus identify the areas with high conservation values. In this thesis, I examine the influence of six major environmental variables on the distribution and habitat suitability of global coral reefs; they are temperature, aragonite saturation state, salinity, nitrate, phosphate, and light.

1.2 Impacts of temperature on coral reefs

Temperature profoundly affects corals both physiologically and ecologically. In aquatic animals (e.g. molluscs, fishes), temperature-dependent performance, such as growth, shows a maximum close to the upper limit of their thermal tolerance. Performance falls under cooling and warming (Pörtner 2002, 2008; Pörtner and Knust 2007). Calcification initially increases with temperature, reaches a maximum and then it declines rapidly at higher temperatures (Jokiel and Coles 1977; Marshall and Clode 2004; Cooper et al. 2008). The optimal temperature for coral performance is species and location dependent. Skeletal growth of the Hawaiian reef corals *Pocillopora damicornis*, *Montipora verrucosa* and *Fungia scutaria* occurs near 26°C (Jokiel and Coles 1977). The optimum temperature for the calcification of hermatypic coral *Pocillopora verrucosa* in the Red Sea is 28-29°C (Sawall et al. 2015). The maximum calcification rate occurs at about 25°C for *Galaxea fascicularis* at Heron Island in the Great Barrier Reef.
(GBR) (Marshall and Clode 2004) and at 26.7°C for massive Porites in the northern GBR (Cooper et al. 2008).

Reef-building corals appear to be living close to their upper thermal tolerance limits (Glynn and D’Croz 1990; Glynn 1993). When corals experience temperatures 1°C above the maximum summertime averages (i.e. bleaching threshold) (Glynn and D’Croz 1990), they can lose their zooxanthellae and/or loss-of-photosynthetic-pigment within zooxanthellae, causing the corals to turn white, a process known as coral bleaching. Mass coral bleaching can eventually lead to coral mortality (Cook et al. 1990; Glynn 1991; Hoegh-Guldberg and Salvat 1995; Berkelmans and Oliver 1998; Berkelmans et al. 2004; O’Farrell and Day 2006; Wilkinson and Souter 2008; Eakin et al. 2010; Pandolfi et al. 2011). Models predict that higher ocean temperatures will increase the number and severity of mass bleaching events in many reefs worldwide (Hoegh-Guldberg 1999; Sheppard 2003; McWilliams et al. 2005).

The mechanism of temperature-induced coral bleaching can be explained by the photoinhibition model (Jones et al. 1998; Hoegh-Guldberg 1999). Thermal stress first damages the dark reactions of photosynthesis by blocking the electron flow to NADP reductase (Jones et al. 1998), leading to an interruption of the light energy flow from the light reactions to dark reactions (Hoegh-Guldberg 1999). The energy then retains in the light reactions rather than being passed to dark reactions (Hoegh-Guldberg 1999). The absorption of excess energy in the presence of oxygen generates the oxygen radicals, which are normally inactivated by the enzymes superoxide dismutase, catalase, and ascorbate peroxidase (Lesser 1997). However, the activities of antioxidant enzymes are unlikely to be sufficient under conditions of elevated temperature (Lesser 1997; Murata et al. 2007). Accumulated oxygen radicals result in impairment of Photosystem II (PSII) in thylakoid (Jones et al. 1998; Warner et al. 1999) and cellular damage, including lipid peroxidation, protein oxidation and DNA degeneration (Lesser 2006), increased susceptibility of zooxanthellae to photoinhibition (Lesser 1997; Hoegh-Guldberg 1999), photodamage, and the subsequent expulsion of zooxanthellae (Smith et al. 2005; Weis 2008). Elevated temperatures can, moreover, suppress coral performance even below the bleaching threshold. The massive reef-building coral Diplodactyla heliopora in the central Red Sea shows no signs of thermal stress, but the growth of healthy colonies has declined by 30% since 1998 with rising temperature (Cantin et al. 2010).

Cold temperature can also negatively affect coral physiology, as indicated by decreased photosynthetic efficiency, reduced pigment concentrations and loss of
zooxanthellae (Saxby et al. 2003; Kemp et al. 2011). The lower thermal limit for coral reefs has long been suggested to be 18°C (Vaughan 1916). Crossland (1984) reported that metabolic activity of coral *Acropora formosa* in Western Australia ceased at 17.7°C (Crossland 1984). Although, Calcification of *Montastraea annularis* in the Gulf of Mexico ceased at 23.7°C, and conspecific corals in the Caribbean Sea ceased at 25.5°C (Carricart-Ganivet 2004; Paz-García et al. 2012). Extreme low temperatures also lead to coral bleaching and mortalities (Coles and Fadlallah 1991; Hoegh-Guldberg et al. 2005; Lajeunesse et al. 2010; Kemp et al. 2011; Lirman et al. 2011; Colella et al. 2012). The mechanism of cold temperatures’ effect on corals is similar to those seen when corals are exposed to high temperatures (Saxby et al. 2003). Given that enzyme activities are temperature dependent (Peterson et al. 2007), decreasing temperatures are likely to decrease the activities of enzymes such as Rubisco (Yamori et al. 2006) that catalyse the dark reactions and the antioxidant enzymes involved in light reactions. Reduced temperatures then lead to an accumulation of oxygen radicals in the presence of light.

In addition, temperature can affect corals by increasing the spread of coral disease. Decimation of coral *acroporid* in the Caribbean was attributed to white band disease (Aronson and Pretch 2001). The growing prevalence of coral disease has been linked to rising temperatures (Jones et al. 2004; Selig et al. 2006; Boyett et al. 2007; Brandt and Mcmanus 2009; Maynard et al. 2011; Randall et al. 2014).

### 1.3 Impacts of ocean acidification on coral reefs

The ocean is the largest sink for anthropogenic carbon dioxide (CO₂), taking up 48% of the total emissions from fossil-fuel (coal, petroleum, and natural gas) and cement-manufacturing between 1800 and 1994 (Sabine et al. 2004). It is estimated that the total oceanic uptake of anthropogenic CO₂ is 118 ± 19 Pg C (Sabine et al. 2004). The annual oceanic uptake rate was estimated at 2.5 ± 0.5 Gt C yr⁻¹ between 2003 and 2012 (Le Quéré et al. 2014). Excess CO₂ enters the ocean and reacts with seawater to create carbonic acid (H₂CO₃), which release hydrogen ions (H⁺) into the seawater, increasing the acidity of the seawater and lowering its pH. This process of declining pH is called ocean acidification (Caldeira and Wickett 2003). Ocean acidification has negative impacts on coral calcification (Doney et al. 2009a).

Ocean acidification involves a series of chemical reactions. Increased atmospheric CO₂ dissolve into the surface seawater, which increases the levels of
CO₂ in aqueous form (CO₂(aq)). This aqueous form of CO₂ (CO₂(aq)) reacts with seawater (H₂O) to form carbonic acid (H₂CO₃) (Doney et al. 2009b) (Eq. 1).

\[
\text{CO}_2^{(aq)} + \text{H}_2\text{O} \leftrightarrow \text{H}_2\text{CO}_3
\]  

(1)

Carbonic acid rapidly dissociates to produce bicarbonate ions (HCO₃⁻) and hydrogen ions (H⁺) (Eq. 2)

\[
\text{H}_2\text{CO}_3 \leftrightarrow \text{HCO}_3^- + \text{H}^+
\]  

(2)

Excess of hydrogen ions (H⁺) in Eq. 2 react with carbonate ions (CO₃²⁻) to form bicarbonate ions (HCO₃⁻) (Eq. 3)

\[
\text{H}^+ + \text{CO}_3^{2-} \leftrightarrow \text{HCO}_3^-
\]  

(3)

Combining Eq. 1 to 3, the net affect is reduced pH and carbonate ion concentration (Doney et al. 2009b).

Ocean acidification decreases the amount of carbonate ions in the seawater. Under the IPCC “Business as Usual” scenario, the surface ocean carbonate ions concentration will decrease by 55% in the year 2100 compared to the pre-industrial concentration (Brewer 1997). The carbonate ions are the fundamental building blocks for the shells and skeletons made from calcium carbonate of numerous marine calcifying organisms (e.g. corals, coralline algae, pteropods, and coccolithophorids) (Eq. 4).

\[
\text{Ca}^{2+} + \text{CO}_3^{2-} \leftrightarrow \text{CaCO}_3
\]  

(4)

Reduction in carbonate ions hinders the calcifying process of organisms (Eq. 4) (Orr et al. 2005). The calcium carbonates that corals secrete for skeletons are aragonite. Decreasing carbonate ions produces a decline in the aragonite saturation state (Ω_{ara}), which is defined as the product between calcium concentrations and carbonate concentrations in the seawater divided by the stoichiometric solubility product of aragonite (K_{spa}) at in situ temperature, salinity, and pressure (Mucci 1983) (Eq. 5).

\[
\Omega_{\text{ara}} = \frac{[\text{Ca}^{2+}][\text{CO}_3^{2-}]}{K_{\text{spa}}}
\]  

(5)

The calcium concentration [Ca²⁺] in seawater is approximately 100 times that of carbonate concentration [CO₃²⁻] and is relatively constant. Therefore, variations
in $\Omega_{\text{ara}}$ are determined by carbonate concentration [CO$_3^{2-}$] (Tyrrell 2008). When $\Omega_{\text{ara}} > 1$, seawater is supersaturated with respect to aragonite, whereas $\Omega_{\text{ara}} < 1$ corresponds to undersaturation of the seawater (Zeebe and Wolf-Gladrow 2001).

Coral tissues are made of two single-cell-thick epithelial layers, the ectoderm and the endoderm (Gattuso et al. 1999). The mechanism by which carbonate ions are transported from seawater through two epithelial layers to the coral calcification cite is not fully understood (Comeau et al. 2013a; Jokiel 2015; Zoccola et al. 2015). However, experimental and field studies have shown that decreased $\Omega_{\text{ara}}$ due to ocean acidification results in the decline of coral calcification (Gattuso et al. 1998; Langdon et al. 2000; Leclercq et al. 2002; Ohde and Hessain 2004; Marubini et al. 2008; Ries et al. 2010; Mollica et al. 2018). Moreover, ocean acidification can reduce coral linear extension and skeleton density. In a mesocosm experiment, the coral Montipora capitata from Hawaii has shown 14% reductions in linear extension rate of under acidified conditions (Jokiel et al. 2008). Mollica et al. (2018) collected coral Porites from four Pacific reefs and showed that skeletal density is directly sensitive to ocean acidification (Mollica et al. 2018).

Scleractinian corals and calcareous green and red algae are important to the building and cementation of the massive reef framework. Reduction in calcification of scleractinian corals due to ocean acidification decreases contributions to CaCO$_3$ production in coral reefs. In addition, reef dissolution may be more sensitive to ocean acidification (Andersson et al. 2009; Silverman et al. 2009; Eyre et al. 2014). Calcium carbonate production must exceed the losses through physical, chemical, and biological erosion to maintain coral reefs in a state of net accretion. Ocean acidification thus may cause coral reef to shift from net accretion to net dissolution (Andersson and Gledhill 2013). The aragonite saturation state of 3.3 is reported as a lower threshold for net carbonate accretion (Kleypas et al. 1999b). Recently, global reefs are predicted to experience net dissolution when $\Omega_{\text{ara}}$ reaches 2.92 (Eyre et al. 2018).

1.4 Impacts of salinity on coral reefs

Reef-building corals are found in seawater with stable salinity conditions. However, coral reefs are frequently exposed to variations in seawater salinity due to major rainfall events, freshwater runoff, storms, periods of prolonged drought or desalination processes (Ferrier-Pagès et al. 1999; Kerswell and Jones 2003; Chartrand et al. 2009; Hédouin et al. 2015). Scleractinian corals are
considered to be osmoconformers with limited ability to adjust to salinity fluctuations (Hoegh-Guldberg and Smith 1989a; Ferrier-Pagès et al. 1999). Small variations in salinity from a control value of 38 psu to 34, 36, and 40 psu significantly reduced the gross production to respiration ratio ($P_g$/$R$) of coral *Stylophora pistillata* and corals died at 40 psu (Ferrier-Pagès et al. 1999). However, coral *Siderastrea siderea* can maintain their photosynthetic and respiratory rates when salinity slowly change within 10 psu range above or below the acclimation value (Muthiga and Szmant 1987). *Porites lutea* and *Pocillopora damicornis* both showed decreased $P_g$/$R$ ratio when salinity suddenly decrease from 30 psu to 10 psu (Moberg et al. 1997). Reduction in salinity from 37 psu to 20.5 psu caused a marked reduction in efficiency (the ratio of variable [$F_v$] to maximal [$F_m$] fluorescence) for coral *Stylophora pistillata* (Kerswell and Jones 2003). Coral *Siderastrea radians* exhibited great tolerance when salinity decreased 2 psu per day from 30 psu to 15 psu, whereas it showed a significant reduction in $F_v$/$F_m$ at 10 psu (Chartrand et al. 2009). Reducing salinity from 35 psu to 23 psu caused death in corals *Stylophora pistillata* and *Seriatopora hystrix*, although moderately reduced salinity of 5 psu did not affect corals (Hoegh-Guldberg and Smith 1989b). In summary, changes in salinity may affect corals metabolism and survival capacities.

A possible mechanism by which hypo-saline conditions affect coral metabolism is that corals contract their polyps in order to minimise contact with the low salinity water (Muthiga and Szmant 1987). Contraction was observed in corals under low salinity (Shumway 1978; Moberg et al. 1997; Ferrier-Pagès et al. 1999). Contraction leads to decline in photosynthesis due to reduced exposure of the zooxanthellae to light and reduced gas exchange that cause a decline in respiration. Reduced salinity can also trigger coral bleaching due to loss of algal symbiosis and/or pigment concentration within symbiosis (Kerswell and Jones 2003). Extremely low-salinity can cause mortality and sloughing of the coral tissues (Kerswell and Jones 2003; Downs et al. 2009). Corals in Persian Gulf survive in salinity of 48-50 psu (Coles 2003). It is reported that corals can tolerate long-term exposure to high salinity by major restructuring of the coral microbiome with *Pseudomonas veronii* as the most abundant bacterium taxon (Röthig et al. 2016). A more recent study suggested that *Symbiodinium* cells can produce high levels of the osmolyte floridoside when exposed to high salinity both in vitro and in their coral host, therefore increasing their capacity to cope with osmotic stress (Ochsenkühn et al. 2017). Thus, low salinity can cause more severe negative impacts on coral metabolism than high salinity (Lirman and Manzello 2009).
1.5 Impacts of nitrate and phosphate on coral reefs

Depending on the symbiotic relationship between corals and zooxanthellae, corals can thrive in oligotrophic conditions. Excess anthropogenic nutrient enrichment is often associated with coral decline (Fabricius 2005; De’ath and Fabricius 2010) and can affect corals and coral reef systems at different levels. At coral physiological level, zooxanthellae in reef corals are typically nitrogen-limited (Cook and D’elia 1987; Fabricius 2005). Elevated dissolved inorganic nitrogen (DIN) can increase zooxanthellae population growth and photosynthetic rates (Dubinsky et al. 1990; Snidvongs and Kinzie 1994; Marubini and Davies 1996; Fabricius 2005; Ezzat et al. 2015), which may induce a significantly reduced carbon fixation rate and low carbon translocation to coral host (Marubini and Davies 1996; Ezzat et al. 2015). *Porites porites* and *Montastrea annularis* have reduced calcification with elevated nitrate by up to 50% when nitrate concentration is higher than 1 μmol L\(^{-1}\) (Marubini and Davies 1996). Coral *Stylophora pistillata* maintained constant growth rates under 10 μmol L\(^{-1}\) NH\(_4\), with 60% reduced growth with NH\(_4\) up to 20 μmol L\(^{-1}\) (Ferrier-Pagès et al. 2000). However, high nitrate or ammonium concentrations (20 μmol L\(^{-1}\)) did not reduce the growth of coral *Porites porites* in the presence of additional bicarbonate (2 μmol L\(^{-1}\)) (Marubini and Thake 1999). The varied coral responses to DIN indicate that the effect of DIN on coral growth rate or calcification is DIN species and concentration dependent. Moreover, increased nitrate concentration alone (Wooldridge 2009a, 2009b), and coupled with phosphorus starvation result in a destabilization of symbionts' membrane, increasing the susceptibility of corals to bleaching (Wiedenmann et al. 2013).

In contrast to DIN, dissolved inorganic phosphate (DIP) enrichment did not increase population density of zooxanthellae (Fabricius 2005). Coral *Acropora aspera* and *Acropora longicyathus* showed no effect of calcification with elevated phosphate up to 2 μmol L\(^{-1}\) (Koop et al. 2001). However, Koop et al. (2001) reported increased coral *Acropora longicyathus* calcification due to phosphorus additions of 2 μmol L\(^{-1}\), while *Stylophora pistillata* and *Pocillopora damicornis* decreased calcification at phosphate concentration higher than 1.2 μmol L\(^{-1}\) (Snidvongs and Kinzie 1994). Phosphate enrichment (2 μmol L\(^{-1}\)) primarily caused the reduced reef calcification at One Tree Island (Kinsey and Davies 1979). The response of corals to nutrient enrichments are dependent on phosphate-dose levels and coral species (Koop et al. 2001). However, it is generally accepted that elevated phosphate can decrease skeletal density, which makes corals more susceptible to breakage (Koop et al. 2001; Dunn et al. 2012). The mechanism of reduced calcification at higher phosphate is thought to be related to reduced CaCO\(_3\) crystal formation in the presence of phosphate.
(Simkiss 1964). However, this mechanism is not fully understood (Snidvongs and Kinzie 1994; Marubini and Davies 1996; Fabricius 2005). Low phosphate concentration can affect the lipid composition of membranes in plants (Essigmann et al. 1998; Frentzen 2004), presumably leading to malfunction of photosynthetic apparatus in zooxanthellae (Tchernov et al. 2004; Wiedenmann et al. 2013). In conclusion, the physiological responses of coral to elevated nutrients are summarised as follows: very low nutrient levels are sub-optimal for corals, and corals can benefit from a slight enrichment, however, higher concentrations of nutrients can have fatal effects on these organisms (D’Angelo and Wiedenmann 2014).

At the ecosystem level, nutrient enrichment decreases the net community calcification and the community shifts from net accretion to net dissolution (Silbiger et al. 2018). Nutrient enrichment promotes algal growth (Anderson et al. 2002; Davidson et al. 2014), which compete with corals for space and light. Excess nutrients increased filamentous algae growth in the Gulf of Eilat (Aqaba), resulting in extensive coral death (Genin et al. 1995). Algal overgrowth on corals often happens after coral mortality in combination with reduced levels of herbivory (Szmant 2002). Furthermore, settlement of all coral larvae was reduced in nitrogen treatments (Koop et al. 2001), which thus reduced coral reef resilience. Nutrient enrichments, in addition, increased the spread of coral disease (Bruno et al. 2003; Voss and Richardson 2006).

1.6 Impacts of light on coral reefs

Most hermatypic corals contain zooxanthellae. More than 90% of the carbon fixed by zooxanthellae via photosynthesis is transferred to the coral hosts to meet their metabolic needs (Falkowski et al. 1984; Muscatine et al. 1984). It is well accepted that scleractinian corals calcify significantly faster in the light than in the dark (Gattuso et al. 1999), an aspect known as light-enhanced calcification (LEC). There are several hypotheses that can explain LEC. First, photosynthesis by zooxanthellae consume CO₂, leading to decreased CO₂ partial pressure, increased pH, and increased carbonate saturation, thus favouring CaCO₃ precipitation (Goreau 1959). Second, protons produced by calcification are removed from calcifying fluid by Ca²⁺-ATPase (stoichiometry: 1Ca²⁺/2H⁺). This favours CaCO₃ precipitation in calcifying fluid, and consequently calcification also produces CO₂, which favours photosynthesis of zooxanthellae by increasing the coelenteric CO₂ reservoir (McConnaughey and Whelan 1997; Gattuso et al. 1999). Third, a light-dependent alkaline coelenteric space, which may facilitate the diffusion of H⁺ produced by CaCO₃ precipitation from calcifying fluid to
coelenteron, can lead to the enhancement of calcification (Furla et al. 1998). Fourth, fixed carbon and O₂ from photosynthesis can be used as fuel to increase ion pumping and elevate the saturation state, which could increase calcification and coral metabolism (Goreau 1959; Pearse and Muscatine 1971; Rinkevich and Loya 1984). Fifth, zooxanthellae synthesise organic matrix molecules or precursors and the organic matrix is assumed to be essential for controlling the formation of CaCO₃ crystals (Allemand et al. 2004). Sixth, phosphate can be reduced in the presence of zooxanthellae, which favours CaCO₃ crystal formation (Simkiss 1964). Irrespective of the exact mechanism underlying the light-enhanced calcification, light environment plays a central role as the engine of coral growth and calcification. Therefore, the reef corals are restricted to the shallow sunlit euphotic zone, where light exceeds 1% of its surface intensity.

Light is a key factor in shaping the vertical distribution of corals. Light intensity declines exponentially with depth in the ocean. Zooxanthellae in deep-water corals have lower respiration rate, light-saturated rate of photosynthesis (P_max), compensation light intensity (E_c), and light intensity of incipient saturation (E_k) compared to the shallow-water corals (Falkowski and Dubinsky 1981; Mass et al. 2007). In contrast, zooxanthellae in deep-water corals have higher pigment content or higher zooxanthellae density in coral tissue than shallow-water corals, which allow them to have higher efficiency of photosynthesis (α) (Dubinsky et al. 1984; Titlyanov et al. 2001; Mass et al. 2007). Concomitantly, deep-water corals tend to have a planar, two-dimensional architecture in order to maximise light harvesting (Mass et al. 2007). Beside light intensity, the spectral composition of light also changes with depth. Shallow coral experience high intensity of UVR and full-spectrum light, while the deep-water corals experience low levels of spectrally enriched blue light. Shallow water corals show higher photosynthetic performances under full-light spectrum (Mass et al. 2010). Additionally, blue light can affect coral circadian-clock genes (Gorbunov and Falkowski 2002).

The relationship between photosynthesis versus light and calcification versus light in corals follows hyperbolic tangent function (Chalker 1981). The rate of photosynthesis or calcification initially increases proportional to irradiance. Thereafter, the rate of photosynthesis or calcification reaches a maximum. However, exposure to excessive irradiance can lead to photoinhibition and coral bleaching (Gleason and Wellington 1993; Niyogi 1999). Photodamage results from the oxidative stress due to the accumulation of reactive oxygen species (ROS) and ROS can damage lipids, protein and DNA and lead to the expulsion of zooxanthellae (Lesser 2006).
1.7 Combined impacts of multiple factors on coral reefs

Coral reefs are exposed to multiple environmental factors that can change simultaneously. It is crucial to understand how these factors interact with each other. There are three broad categories of the combined outcome of multiple factors, they are (1) additive (when the combined effect is equal to the sum of individual effects), (2) antagonistic (when the combined effect is less than the sum of individual effects), and (3) synergistic (when the combined effect is greater than the sum of individual effects) (Folt et al. 1999). In both theoretical and applied research, the combined effect of multiple factors is often assumed to be additive (Halpern and Fujita 2013). If multiple factors, such as temperature with nutrients or temperature with acidification, interact synergistically (e.g. (Reynaud et al. 2003; Wooldridge 2009a; Wiedenmann et al. 2013; Prada et al. 2017)), predictions based on additive expectations will underestimate the overall ecological impacts on coral reefs. If multiple factors act independently, additive models may be suitable. However, if multiple factors interact antagonistically, predictions based on additive expectations will overestimate the overall ecological impacts. Non-additive effects may be as common as additive ones (Crain et al. 2008; Darling and Côté 2008). The additive model is therefore inappropriate when factors interact synergistically or antagonistically. However, predicting combined effects of multiple factors is complicated and challenging because (1) the response of species may vary when the additional factor is at a different level; (2) interaction of factors is species dependent; (3) community response to stressors can differ due to changing interactions between species under different stressor scenarios (Crain et al. 2008). Factors that interact in a non-additive manner can lead to “ecological surprises” producing sudden and accelerated declines in biodiversity and ecological function (Paine et al. 1998; Ostrander et al. 2000).

1.8 Research objectives

The overall goal of this thesis was to investigate the effects of environmental factors on the global distribution of coral reefs and to quantify habitat suitability for coral reefs. This thesis addresses the following specific aims:

1. What are the suitable environmental ranges for potential coral reef habitats?
2. How does reef habitat suitability respond to environmental factors?
3. How does habitat suitability change when regional adaption is taken into account?
4. How does habitat suitability change under global warming and ocean acidification?
5. Does the potential coral reef habitats remain unchanged under global warming and ocean acidification in the future?
6. What are the combined effects of pairwise factors, additive or non-additive?
2 Suitable environmental ranges for potential coral reef habitats in the tropical ocean

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Abstract

Coral reefs are found within a limited range of environmental conditions or tolerance limits. Estimating these limits is a critical prerequisite for understanding the impacts of climate change on the biogeography of coral reefs. Here we used the diagnostic model ReefHab to determine the current environmental tolerance limits for coral reefs and the global distribution of potential coral reef habitats as a function of six factors: temperature, salinity, nitrate, phosphate, aragonite saturation state, and light. To determine these tolerance limits, we extracted maximum and minimum values of all environmental variables in corresponding locations where coral reefs are present. We found that the global, annually averaged tolerance limits for coral reefs are 21.7-29.6°C for temperature, 28.7-40.4 psu for salinity, 4.51 μmol L⁻¹ for nitrate, 0.63 μmol L⁻¹ for phosphate, and 2.82 for aragonite saturation state. The averaged minimum light intensity in coral reefs is 450 μmol photons m⁻² s⁻¹. The global area of potential reef habitats calculated by the model is 330.5 × 10³ km². Compared with previous studies, the tolerance limits for temperature, salinity, and nutrients have not changed much, whereas the minimum value of aragonite saturation in coral reef waters has decreased from 3.28 to 2.82. The potential reef habitat area calculated with ReefHab is about 121×10³ km² larger than the area estimated from the charted reefs, suggesting that the growth potential of coral reefs is higher than currently observed.

2.1 Introduction

Tropical coral reefs are among the most diverse ecosystems on Earth and have an enormous social and economic importance (Moberg and Folke 1999; Cesar and Chong 2004). They account for less than 0.2% of the global ocean area (Lalli and Parsons 1997; Spalding et al. 2001) but provide habitats to about a quarter of all marine species (Thornhill 2012). They also provide goods and services to humans (Martínez et al. 2007). The fitness of tropical corals depends on several environmental variables including temperature, salinity, nutrients, aragonite saturation state, and light. Like many other ecosystems, coral reefs are endangered by global environmental changes such as eutrophication, sea level rise, global warming, and ocean acidification (Hoegh-Guldberg et al. 2007; Carpenter et al. 2008).

In the last decades, many studies have documented the impacts of climate change on different coral reef ecosystems around the globe (see Dubinsky & Stambler, 2011, for an updated collection of studies) (Dubinsky and Stambler
2011). It is well established, for example, that rising sea temperature can cause widespread damage to reefs (Lesser 2004; Diaz-Pulido et al. 2009). During the 20th century, the global surface average temperature has increased by 0.74°C (IPCC 2007) and, concomitantly, temperature-driven bleaching events have increasingly been reported (Burke et al. 2011). Besides an upper thermal tolerance limit, corals are also affected by a lower temperature threshold (Jokiel and Coles 1977; Guinotte et al. 2003; Castro and Huber 2007; Couce et al. 2012). Other factors, such as salinity, nutrient concentrations, and aragonite saturation state can also affect coral growth (Ferrier-Pagès et al. 1999, 2000; Marubini et al. 2008). Quantifying the responses of coral reefs to different environmental changes is therefore required to better understand their biogeography.

One of the first attempts to quantitatively predict the biogeography of coral reef global habitats on a global scale is represented by the works of Kleypas (Kleypas 1995, 1997) with the use of the diagnostic model ReefHab. Using ReefHab in combination with environmental variables available up to the late ‘80s and early ‘90s, Kleypas (Kleypas 1997) estimated the potential area of coral-reef habitat in tropical and subtropical regions. Since then, new marine environmental data are available. These new data can help to produce an updated view of potential reef habitats and can enable us to derive new tolerance limits for coral-reef habitats with respect to different environmental variables.

Here we use the ReefHab model in combination with the latest available environmental data and high-resolution bathymetry to predict the present day potential reef habitats for coral growth at the global scale. Our predictions are then discussed in the context of the actual observations of coral reef occurrences. Finally, by using ReefHab in an inverse mode, we determine new suitable environmental limits for coral reefs.

2.2 Materials and Methods

2.2.1 ReefHab model and environmental data

We use the diagnostic model ReefHab (Figure 2.1), which we coded in Python, to calculate the potential reef habitats for coral growth in the global ocean between 40° N and 40° S. The model uses climatological data of temperature (T), salinity (S), nitrate (NO$_3^-$), and phosphate (PO$_4^{3-}$) from the first 5 m water depth obtained from the World Ocean Atlas (WOA) 2009 (Antonov et al. 2010; Garcia et al. 2010; Locarnini et al. 2010) at a 1° × 1° spatial resolution (available at
Alkalinity and Dissolved Inorganic Carbon (DIC) at a 1° × 1° spatial resolution (Key et al. 2004) (available at http://cdiac.ornl.gov/ftp/oceans/GLODAP_Gridded_Data/ in netCDF format) are used to calculate the aragonite saturation state (Ωarag) with the software CO2SYS (Lewis and Wallace 1998), coded in Python. All these variables are shown in Figure 2.2.

Figure 2.1 Flow chart of the ReefHab diagnostic model. Modified from Kleypas (1997).

The maximum depth of reef growth (Zmax) is determined using the equation:

\[
Z_{\text{max}} = \frac{\ln(I_{\text{min}} / \text{PAR})}{K_{490}}
\]

(1)

where \(I_{\text{min}}\) is the minimum light intensity necessary for reef growth (in mmol photons m\(^{-2}\) s\(^{-1}\)), PAR (in mmol photons m\(^{-2}\) s\(^{-1}\)) is the average photosynthetically available radiation at sea surface, and \(K_{490}\) (in m\(^{-1}\)) is the attenuation coefficient of light at wavelength 490 nm. Both PAR and \(K_{490}\) are from SeaWiFS Level 3 data (available at http://oceancolor.gsfc.nasa.gov/cgi/l3) and have a spatial resolution of 5′ × 5′. The model calculates \(Z_{\text{max}}\) in each 5′ × 5′ grid cell. This information is then used in combination with the high-resolution
(30” × 30”) bottom topography data from the General Bathymetric Chart of the Oceans (the GECBO_08 Grid, version 2010, available at http://www.gebco.net in netCDF format) to check for the light criteria. The smallest 5’ × 5’ grid cell of PAR and K₄₉₀ data is therefore subdivided into 100 cells of 30” × 30” resolution to match with bathymetry.

The model checks every 1° × 1° grid cell of the 360 × 80 matrix if temperature, salinity, nitrate, phosphate, and Ωₐra are within the specified ranges for potential reef habitat and every 30” × 30” grid cell of the 43200 × 9600 matrix if also the light condition is suitable. If all these variables are within the suitable ranges, the model produces a positive result in terms of suitable reef habitat at the given location. Otherwise, if any of these environmental variables is not in the suitable range, a negative result (i.e. unsuitable reef habitat) is generated (Figure 2.1). Ωₐra is not checked for in the Indonesian Sea and in the Caribbean because GLDAP does not contain DIC and alkalinity data in these regions. ReefHab predicts potential reef habitats at the same resolution as the topography dataset (30” × 30”) because water depth variations occur over small scales and exert a strong control over reef distribution. The spatial resolution of the environmental variables is much coarser (1° × 1°); however, these data do not vary considerably within their respective resolutions. The model results are finally presented on a 1° × 1° spatial resolution map and the percentage of potential reef habitat is calculated based on the percentage of positively evaluated 30” × 30” grid cells falling within a 1° × 1° grid cell.

Our results are compared with the works of Kleypas (Kleypas 1997; Kleypas et al. 1999b), which reproduced the potential reef habitat of the early ’90s, by using temperature (Reynolds and Marsico 1993), salinity (Levitus et al. 1994), nutrients (Levitus et al. 1993), water depth (Sloss and W. 1986), PAR (Pinker and Laszlo 1992), and K₄₉₀ (Arnone et al. 1992) with spatial resolutions of, respectively, 1° × 1°, 1° × 1°, 1° × 1°, 5’ × 5’, 2.5° × 2.5°, and 0.16° × 0.16°. The temporal resolution of temperature was weekly, all the other variables had monthly resolutions. Our study, however, predicts potential reef habitats based on the newest available environmental and topography data. In addition, we modified ReefHab by including a check on the aragonite saturation state.
Figure 2.2 Environmental data used by the ReefHab model. Temperature, salinity, and nutrient data are taken from the World Ocean Atlas (WOA) 2009 and have a 1° × 1° spatial resolution. PAR and K490 are from SeaWiFS Level 3 data, have a 5° × 5° spatial resolution, and are used to calculate $Z_{max}$ at $I_{min} = 450 \mu$mol photons m$^{-2}$ s$^{-1}$. Alkalinity and DIC are taken from GLODAP, have a 1° × 1° spatial resolution and are used to calculate $\Omega_{ar}$.

2.2.2 Reef location data

The model results (i.e. the potential reef habitats predicted with ReefHab) are qualitatively compared against charted reef observations of the Global Distribution of Coral Reefs 2010 (Spalding et al. 2001; IMaRS-USF (Institute for Marine Remote Sensing-University of South Florida) 2005; IMaRS-USF IRD (Institut de Recherche pour le Developpement) 2005) (available at http://data.unep-wcmc.org/datasets/13 as DBF data, which we transformed in HDF). These observations have been compiled from a variety of sources. Deep and cold water corals are not included in this study. The majority of the data, 85%, originates from the Millennium Coral Reef Mapping Project and are mapped at a 30 m resolution. Of this large data fraction, only 35% has been validated (Andréfouët et al. 2006). The remaining 15% of the data were compiled from other sources, including the World Atlas of Coral Reefs (Spalding et al. 2001). Although this dataset has limitations, for example for some reef structure smaller than 30 m and in turbid areas, and despite the fact that only a
small portion of it has been validated (Andréfouët et al. 2006), it still represents the best and most used information available to date (van Hooidonk et al. 2014; Wood et al. 2014). In this dataset, coral-reef areas are recorded as polygons. By overlaying these polygons on the available bathymetric profile (GEBCO_08) we created an "observed" reef habitat distribution on a 30” × 30” grid cell resolution. Every 30” × 30” grid cell that contains one or more points that constitute a coral-reef polygon is marked as observed reef habitat. For comparability with the coarse resolution environmental data, we calculated the percentage of observed reef habitats based on the number of 30” × 30” grid cells containing coral reefs within a 1° × 1° grid cell.

2.2.3 Derivation of suitable environmental ranges for coral-reef habitats

To find the suitable environmental ranges for coral-reef habitats in today’s ocean, we used the model in an inverse mode, as explained in the following. We identified the values of annual temperature, salinity, nitrate, phosphate, and irradiance at each location (i.e. each grid cell) where observations showed the presence of reefs. We then considered the global maximum and minimum values of each environmental variable. These values represent the average environmental ranges for observed coral reefs and are later used with the model to predict the potential reef habitats, i.e. all those locations of the oceans, besides those already known from the observation, that can potentially host coral reefs.

The overlay of the observed reef locations with the GEBCO_08 bathymetry revealed inconsistencies between ocean depth and reef occurrence by showing the presence of coral reefs in waters deeper than 2000 m and up to 6000 m (see Supporting Information Figure A.1). Such inconsistencies remained even when using different bathymetry data (SRTM30, from ftp://topex.ucsd.edu/pub/srtm30_plus/). The calculation of the minimum irradiance ($I_{\text{min}}$) required for coral growth (Equation 1), therefore, produced unrealistically low irradiance levels in locations supposedly associated with the presence of coral reefs but corresponding to very deep waters. In order to determine the most realistic value of $I_{\text{min}}$ and hence circumvent such inconsistencies, we adopted a standard optimization technique. This consisted in systematically varying the value of $I_{\text{min}}$ over a defined range to minimize the number of false negatives, while producing the most reasonable qualitative match between predicted potential reef habitat and actual reef distribution (see below for further details).
In order to analyse how model performance changes when using different tolerance limits, we run the ReefHab model with the most recent environmental datasets (WOA 2009) but in combination with the tolerance limits of Kleypas, hereafter K97 tolerance limits. In addition, we compare and discuss our results against the tolerance limits later suggested by Kleypas et al. (Kleypas et al. 1999b), hereafter K99 tolerance limits.

Finally, our newly derived tolerance limits are determined on the basis of annual climatologies and do not take into account short-term (weekly, monthly, or seasonal) extremes. Although short-term disturbances can have lethal consequences for corals, it is the long-term (decadal) environmental condition that determines the presence/absence of coral reefs and that is relevant to our study. However, for comparability, we also calculated the tolerance limits on the same temporal scales (i.e. weekly and monthly) considered for deriving the K97 and K99 limits.

### 2.2.4 Evaluation of model performance

The evaluation of the model performance consists of two major aspects: 1) the spatial pattern of the predicted potential reef habitats is compared with the observed coral-reef distribution on a $1^\circ \times 1^\circ$ spatial resolution, and 2) the area of predicted potential reef habitats is compared with the area determined from observed reefs.

In order to compare the distribution pattern of predicted potential reef habitats with the observed coral reefs, we produced a $360 \times 80$ matrix of ones and zeros for, respectively, the presence (when the percentage of reef habitat is above 0) and absence of coral reefs (when the percentage of reef habitat equal 0). A similar matrix was produced for the observed coral-reef distribution. By subtracting the matrix of predicted potential reef habitats from the matrix of observed coral reefs, we generated a spatial distribution matrix with -1, 0, and +1. The value -1 represents a false positive (FP), i.e. the model predicts a suitable reef habitat in a grid cell where coral reefs are not observed. The value +1 represents a false negative (FN), i.e. the model does not predict a suitable reef habitat in a grid cell where reefs are actually observed. The value 0 reflects a match between model results and observed reefs and represents both a true positive (TP) and a true negative (TN).

To evaluate the response of the model to changes in $I_{\text{min}}$, we used the Receiver Operating Characteristics (ROC) graph (Fawcett 2006), by plotting the true
positive rate vs. the false positive rate. The true positive rate (TPR) is the ratio between true positives and positives (P), i.e.: 
$$\text{TPR} = \frac{TP}{P} = \frac{TP}{(TP + FN)}.$$ 
The false positive rate (FPR) is the ratio between false positives and negatives (N), i.e.: 
$$\text{FPR} = \frac{FP}{N} = \frac{FP}{(FP + TN)}.$$ 

The data falling on the point TPR=1 and FPR=0 represent a perfect classification (i.e. a perfect model result). The distance to the perfect classification point can thus be used as a measure of the quality of the model results.

### 2.3 Results

#### 2.3.1 Derivation of new tolerance limits

Table 1 summarises our results concerning the derivation of the new tolerance limits for the presence of coral reefs. We found that coral reefs are currently present in waters with annual mean temperature between 21.7°C and 29.6°C and with annual mean salinity between 28.7 psu and 40.4 psu. These values are not very different from those by K97. In contrast, the nitrate threshold above which no corals are found has increased from 2.0 μmol L⁻¹ (K97) to 4.51 μmol L⁻¹ (this study) and the phosphate threshold has increased from 0.2 μmol L⁻¹ (K97) to 0.63 μmol L⁻¹ (this study). Note, however, that the K97 tolerance limits were initially based on values quoted in the literature and subsequently refined visually by comparing predictions of ReefLab with reef locations known at that time (Kleypas 1997). Later, Kleypas et al. (Kleypas et al. 1999b) determined new tolerance limits (K99) with the approach that we have adopted in our study. By using the WOA 2009, we obtain results more similar to K99 than K97 (Table 2.1). We also found that the $\Omega_{\text{ara}}$ threshold below which coral reefs disappear is 2.82, which contrasts with the value of 3.28 suggested earlier by Kleypas et al. (Kleypas et al. 1999b).

As mentioned in the Methods section, the new $I_{\text{min}}$ was determined with a standard optimization technique. When $I_{\text{min}}$ is increased from 50 to 450 μmol photons m⁻² s⁻¹, false positives decrease steadily from 742 to 413, whereas false negatives increase from 14 to 51 (Figure 2.3). From $I_{\text{min}} = 450$ μmol photons m⁻² s⁻¹ to $I_{\text{min}} = 500$ μmol photons m⁻² s⁻¹, false positives further decrease from 413 to 200, whereas false negatives increase rather abruptly from 51 to 327 (Figure 2.3). False positives do not indicate an erroneous result because the model estimates if reefs can "potentially" occur. In contrast, false negatives are to be avoided because they represent the case in which the model fails to predict a suitable habitat in a location where reefs do actually occur.
The model response at different $l_{\text{min}}$ was further analysed with the ROC graph (Figure 2.4). Due to the strong response in false positives and false negatives when $l_{\text{min}}$ changes from 450 to 500 $\mu$mol photons m$^{-2}$ s$^{-1}$, we further investigated the model response in this $l_{\text{min}}$ range with a finer step width of 10 $\mu$mol photons m$^{-2}$ s$^{-1}$. The best TPR to FPR ratio, i.e. the closest value to the perfect classification point (0,1) in the ROC graph, is obtained with $l_{\text{min}} = 450$ $\mu$mol photons m$^{-2}$ s$^{-1}$. 
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Table 2.1: Tolerance limits for coral reefs associated to environmental variables.

- **KRC and K99**: Key references for the data.
**An annual average as reported by the original study**.

\[ 150 \times 10^{-3} \times 35 \text{ for endoscopy use.} \]

New tolerance limits are highlighted in bold. As explained in the main text, K97 refers to the limits suggested by Klippes et al. (1999) and K99 refers to the limits suggested by Klippes et al. (1997).
When ReefHab is run with the K97 tolerance limits, the model produces 473 false negatives. With our newly derived tolerance limits, false negatives are decreased to 51. Note that false negative model decisions could not be totally avoided due to the problems with bathymetry, as described in the supplementary material. The strong decrease in false negatives obtained with our tolerance limits is accompanied by a very minor increase in false positives, from 398 (K97 limits) to 413 (new limits), see Supporting Information S2 and S3.

Figure 2.3 Number of false negatives and false positives obtained at different $I_{\text{min}}$ values. False negatives and false positives steadily increase and decrease, respectively. A sharp shift in both false negatives and false positives is observed at $I_{\text{min}} = 450 \ \mu\text{mol photon m}^{-2} \ \text{s}^{-1}$. 

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Figure 2.4 Receiver Operating Characteristic (ROC) graph. The graph shows the true positive rate versus the false positive rate. $I_{\text{min}} = 450 \mu\text{mol photon m}^{-2} \text{s}^{-1}$ (pink dot) is the nearest to the (0, 1) point in the graph and therefore represents the best model result. The small inset is a zoom of the graph area where all the data points occur. The dashed blue line represents points in which true positive rates equal false positive rates.

2.3.2 Potential reef habitats predicted by new environmental variables and K97 tolerance limits

Figure 2.5 (panels A and B) shows a comparison between the predictions of potential reef habitats, obtained by running ReefHab with the most recent environmental variables (excluding $\Omega_{\text{in}}$) in combination with the K97 tolerance limits, and the observed coral-reef distribution. The model reproduces a reasonable general pattern of potential reef habitats in the tropical and subtropical ocean although with some exceptions. For example, the model overestimates the occurrence of coral reefs in the Mediterranean Sea and it underestimates the occurrence of reefs in the Red Sea and in the Persian Gulf. The model does not capture the coral reefs of the Indian Ocean, Seychelles, Chagos Archipelago, and Maldives. In Southeast Asia, the model underestimates the occurrence of some coral reefs in the Java Sea and the Flores Sea and overpredicts reefs in the central and western coasts of northern Australia. In the
Pacific, the model does not capture some small reefs such as Johnston Atoll, Palmyra Atoll, Tuvalu, Howland Island, and Galápagos Island. The model, however, performs well in the Atlantic/Caribbean region although the occurrence of reefs is overestimated along the Brazilian coasts.

**Figure 2.5** Observed coral reefs (A) and potential reef habitats predicted by ReefHab with the K97 tolerance limits (B) and with the tolerance limits derived in this study (C). All maps are presented on a 1° × 1° spatial resolution. Green rectangular boxes highlight areas where ReefHab overestimates the occurrences of potential reef habitats with respect to observations, while red boxes highlight areas where the occurrences of potential reef habitats are underestimated. The K97 tolerance limits fail to predict potential reef habitats in the Red Sea and Gulf of Aden, in the central Indian Ocean and central Pacific Ocean, and in the Indonesian Sea. These reefs are correctly captured by the new tolerance limits. The potential reef habitats predicted in the Mediterranean with the K97 limits are not produced with the new tolerance limits. Both tolerance limits predicted suitable potential reef habitats along the Brazilian coast, although the presence of reefs there is not confirmed by observations.
2.3.3 Potential reef habitats predicted by new environmental variables and new tolerance limits

The predicted potential reef habitats obtained with the tolerance limits derived in this study (Table 2.1 highlighted in bold) are consistent with the observed coral-reef distribution (Figure 2.5, panels A and C). The model, correctly, does not predict the presence of coral reefs in the Mediterranean Sea, although it overestimates coral reefs in the Gulf of Oman and in the Gulf of Aden. Other places where the model overestimates coral reefs are the Seychelles, Mauritius, and the Andaman Sea. The model performs very well in Southeast Asia, along Australian coasts, in the Pacific Ocean, and in the Atlantic Ocean, especially in the western Pacific, where some small reefs (e.g. Johnston Atoll, Palmyra Atoll, and Tuvalu) that could not be captured with the K97 tolerance limits (see Figures 2.5 & Supporting Information Figure A.3) are now correctly predicted. Reef habitats along the Brazilian and northwestern Australian coasts are still somewhat overestimated (Figure 2.5C).

With the tolerance limits derived in this study (Table 2.1), we estimate a global potential reef habitat area of about $330.5 \times 10^3$ km$^2$. The actual area where coral reefs are observed is about $209.5 \times 10^3$ km$^2$ (Figure 2.6).

![Figure 2.6](image_url)  
**Figure 2.6** Area of potential reef habitats at different $I_{\text{min}}$ values. The blue line represents the observed area covered by reefs; the red line represents the reef area.
estimated by Smith (1978), the yellow line represents the reef area estimated by Spalding & Grenfell (1997), the green line represents the potential reef habitat area estimated by Kleypas (1997), and the light blue line represents the potential reef habitat area estimated by Spalding et al. (2001).

2.4 DISCUSSION

2.4.1 Tolerance limits for coral reefs

Temperature, salinity, nutrients, aragonite saturation state, and light are among the most important factors in controlling the geographic distribution of shallow-water coral reefs (Kleypas et al. 1999b; Couce et al. 2012; Freeman et al. 2013). Global warming, ocean acidification, eutrophication, and other environmental perturbations can thus have negative consequences on corals by changing their habitats. Quantifying the suitable environmental ranges for coral reefs is a critical prerequisite for predicting the distribution of coral reefs in the future and for assessing the impacts that climate change may have on the reef ecosystem. Here we used the diagnostic model ReefHab (Kleypas 1995, 1997) in combination with the most updated environmental data and high resolution bathymetry to derive potential reef habitats in the tropical and subtropical oceans. We found that the presence of several reefs is not predicted (e.g. Seychelles, and Maldives, and reefs in the Java Sea) when the model is forced with the K97 tolerance limits (see Supporting Formation Figure A.2). This is because the K97 limits for nutrients, especially phosphate, are lower than the concentrations observed in those regions. We therefore derived the current environmental ranges suitable for coral reefs by running ReefHab in an inverse mode.

The K97 and K99 limits were provided on different temporal time scales (weekly, monthly and annually averaged). For comparison purposes, we computed the new environmental tolerance ranges on the same time scales although, as explained in the Methods section, our focus lies on the annually averaged conditions that sustain coral reefs. The newly derived limits for temperature are similar to the K97 and K99 limits when using weekly data (Table 2.1). On an annual basis, however, the temperature range resulting from our study (21.7—29.6 °C) is narrower than that obtained with weekly data (15.7—35.5 °C), because extreme values are smoothed out by the longer-term average. Short-term (from hours to weeks) laboratory and field studies have investigated the thermal tolerance for growth in common species of reef-building corals (Jokiel and Coles 1977; Hoegh-Guldberg and Smith 1989b).
While exposure to extreme temperatures for a sufficiently long time induces bleaching (Hoegh-Guldberg 1999; Freeman et al. 2001), and can lead to massive coral mortalities (Glynn 1993; Sheppard 2003; O’Farrell and Day 2006), this occasional perturbation does not necessarily preclude the recovery of the ecosystem and the long-term suitability of the reef habitat (Brown and Suharsono 1990). Only if the frequency of such catastrophic events increases, the habitat may become unsuitable for corals, but this would be reflected in the long-term trend of the observed annual temperatures.

In contrast to the temperature, the tolerance range for salinity that we obtained on a monthly basis is similar to the K99 limits, whereas it is wider than the K97 limits. When calculated on an annual basis, the range becomes narrower than when using the monthly data, because again the values are smoothed by the longer-term average. The upper limit is determined by the Red Sea, which has the highest salinities (up to 41.1 psu) of all ocean waters. Whereas the lower limit is determined by the Gulf of Thailand, which experiences salinity values as low as 25.4 psu during the rainy season. Such broad tolerance limits for salinity are consistent with evidence suggesting that corals’ metabolic performance is only weakly sensitive to changes in this variable (Muthiga and Szmant 1987; Hoegh-Guldberg and Smith 1989b; Moberg et al. 1997; Ferrier-Pagès et al. 1999).

The annual thresholds for nitrate and phosphate that we obtained are up to three times higher than the K97 limits, but similar to the K99 limits (Table 2.1). These higher nutrient thresholds predicted by our study with respect to K97 are associated to the presence of coral reefs in areas adjacent to the Galápagos Islands and are, conceivably, due to deep-water upwelling in that region. When forced with the K97 limits, however, our model produced more false negatives than with our newly derived limits, especially with respect to phosphate. The new limits for nutrients improved the predictions of potential reef habitats in the Indonesian Sea, the central Pacific Ocean, the Seychelles, the Chagos Archipelago, and the Maldives, and they generated more false positives than the K97 limits in the Arabian Sea, the Bay of Bengal, the South China Sea, the central and eastern Pacific, and the Atlantic (see Supporting Information Figure A.2 & A.3).

Kleypas (Kleypas 1997) estimated the minimum light intensity necessary for coral reef habitats ($I_{\text{min}}$) in the range of 250–300 nmol photons m$^{-2}$ s$^{-1}$ by comparing the total reef area predicted by ReefHab with the estimate of Smith in 1978 (Smith 1978). Newer estimates, however, suggest smaller areas for global coral-reef cover (Spalding and Grenfell 1997; Spalding et al. 2001),
which are also in accordance to our results (Figure 2.6). Our optimization procedure suggests that $I_{\text{min}} = 450 \ \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ is a more plausible minimum light threshold for coral-reef habitat in today’s ocean waters. This higher $I_{\text{min}}$ value we found with respect to earlier works produces, consistently, a smaller total coral-reef area than the previous studies (Smith 1978; Kleypas 1997). We also found a trade-off emerging between the accuracy in reef distribution patterns and the potential reef area predicted by the model when varying $I_{\text{min}}$. Specifically, when $I_{\text{min}}$ increases from 50 to 450 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$, the model predictions in terms of both coral-reef distribution patterns and habitat area become more accurate (i.e. less false negatives are produced).

With $I_{\text{min}} = 600 \ \mu\text{mol photons m}^{-2} \text{ day}^{-1}$, the potential habitat area is closest to the observations ($209.49 \times 10^3 \text{ km}^2$ predicted vs. $209.68 \times 10^3 \text{ km}^2$ observed), but such a good match is obtained at the cost of a less accurate prediction of reef distribution patterns (i.e. at the cost of increased false negatives). The minimum light intensity necessary for coral reefs that we found here reflects, therefore, the best balance between distribution patterns and reef area or, in other words, between (1) false predictions, i.e. false positives and false negatives (Figure 2.3), and (2) the correct outcomes, i.e. true positives and true negatives, as inferred from the ROC graph (Figure 2.4). When the sun angle is low, a significant amount of light is reflected from the water surface. Water close to the land has high concentration of suspended materials that affect the clarity of water. Light penetration, thus, obviously varies with latitude and with the distance from shore. The $I_{\text{min}}$ derived in the present study, however, represents a spatially averaged minimum light intensity for coral-reef habitats. Also different coral species can be characterised by different $I_{\text{min}}$ values. *Pocillopora damicornis* from Hawaii, for example, has a higher $I_{\text{min}}$ (Jokiel and Morrissey 1986) than *Pavona praeorta* from the Marshall Islands (Wetley and Porter 1976). And even within the same species, the minimum light tolerance can differ due to morphological reasons (Jokiel and Morrissey 1986). Our study, however, considers the reef community as a whole and the light tolerances reported for some corals (Wetley and Porter 1976; Jokiel and Morrissey 1986), which are lower than what we found here, may not be representative of large natural environments supporting the development of very diverse reef communities. Note also that the $I_{\text{min}}$ found here reflects the minimum irradiance levels required for coral-reef growth as averaged over a whole year. Obviously, the actual light conditions experienced in coral-reef waters can vary strongly on shorter time scales (from seasonal to daily).

Kleypas et al. (1999) suggested a lower threshold for $\Omega_{\text{ara}}$ of 3.28. This limit has been adopted in the literature as “the standard value” below which no reefs occur (Hoegh-Guldberg et al. 2007; Meissner et al. 2012). Our study, however,
suggests a lower threshold of 2.82 and shows that coral reefs in the Gulf of California, Galápagos, and northeast of Australia are found in waters where \( \Omega_{\text{ara}} \) ranges between 2.82 and 3.28. The total reef area in these waters is \( 8.82 \times 10^3 \) km\(^2\), which accounts for about 4.2\% of the global coral-reef coverage. Declining seawater pH due to the absorption of increasing atmospheric CO\(_2\) the process of ocean acidification, reduces carbonate ion concentrations and thus \( \Omega_{\text{ara}} \) (Hoegh-Guldberg et al. 2007). Several studies indicate that coral calcification decreases with declining \( \Omega_{\text{ara}} \) (Gattuso et al. 1998; Langdon et al. 2000; Bruno and Selig 2007; Marubini et al. 2008). In contrast, laboratory experiments show that some scleractinian coral species (e.g. *Oculina patagonica*) can survive acidified conditions (minimum pH = 7.3) for up to one year, although without accreting calcium carbonate (Fine and Tchernov 2007). Other species (*Stylophora pistillata*) can even calcify at \( \Omega_{\text{ara}} \) values as low as 0.68 in the laboratory, albeit at rates lower than when subject to higher \( \Omega_{\text{ara}} \) (Venn et al. 2013). These environmental values, however, do not reflect present day ocean conditions. Consistently with our finding, field investigations in the natural environment suggest that coral reefs approach their natural limit at \( \Omega_{\text{ara}} = 2.9 \) (Fabricius et al. 2011). Unfortunately, the GLODAP dataset for DIC and TA does not cover the Indonesian Sea and the Caribbean. We can therefore not report on the aragonite saturation state in these areas. However, the lower threshold value of \( \Omega_{\text{ara}} \) of 2.82 is found at the northern Great Barrier Reef, which is obviously covered by the GLODAP dataset.

De’ath et al. (2009) showed that coral reefs of the northern Great Barrier Reef (GBR) are experiencing declining calcification rates since 1990 and suggested increasing temperature and declining \( \Omega_{\text{ara}} \) as potential causes. Our results lend weight to their suggestion by showing that waters of the northern Great Barrier Reef are characterized by \( \Omega_{\text{ara}} \) values close to the minimum threshold.

The optimization of the environmental boundary limits for coral-reef habitats helped us to substantially reduce the number of false negatives (i.e. to reduce the number of known coral-reef sites excluded by the model predictions) to only 51 occurrences. Therefore, despite its simplicity, ReefHab predicted the spatial distribution of potential reef habitats with good accuracy as compared to patterns of actual coral-reef occurrences. An earlier study compared the performances of three other models in predicting the presence of coral reefs in shallow tropical waters (Couce et al. 2012). Despite the higher complexities of these models with respect to ReefHab, they tend to produce a higher number of false negatives than ReefHab (for example compare Figure 4 in Couce et al. (2012) with our Supporting Information Figure A.4).
2.4.2 Potential reef habitat area

A precise estimate of the global coral reef habitat area is important for understanding the potential impact of changing environmental conditions on coral-reef biogeography. Different estimates of global coral-reef coverage are found in the literature (Smith 1978; Copper 1994; Kleypas 1997; Spalding and Grenfell 1997; Spalding et al. 2001; Burke et al. 2011), ranging from $250 \times 10^3$ km$^2$ (Burke et al. 2011) to $1500 \times 10^3$ km$^2$ (Copper 1994). The coral-reef area we determined from the newest charted reef data is about $209.5 \times 10^3$ km$^2$. Whether this lower value with respect to earlier estimates is an indication of a global decline in coral-reef cover or an improvement with respect to rather optimistic estimates is not easy to judge.

Our model results suggest a potential reef habitat of about $330.5 \times 10^3$ km$^2$. The model, however, predicts the “potential” reef habitat, which is by definition an overestimation of the “real” coral-reef area. In addition, the ReefHab model predicts potential reef habitats only as a function of six physical and chemical environmental factors: 1) temperature, 2) salinity, 3) nitrate, 4) phosphate, 5) aragonite saturation state, and 6) light. Besides these environmental factors, the world’s coral reefs also face threats from a wide range of human activities, including coastal development, runoff of fertilizer from agricultural activities, physical damages from anchors and ship groundings, overfishing, and tourism. Omitting these difficult to quantify factors may also lead to an overestimation of potential reef habitats with respect to the actual observations. Uncertainties can also affect the actual reef observations. For example, although in some regions the presence of reefs is well known (e.g. in Cape Verde (Moses et al. 2003), Gulf of Guinea (Jones 1994), and our model correctly predicts their presence, these reefs have not yet been charted and therefore do not appear in the observational data. Additionally, new reefs are constantly being discovered (Pohl et al. 2014).

In summary, by using the diagnostic ReefHab model, we were able to predict the global distribution of potential coral-reef habitats based on a number of physical and chemical variables, which then allowed us to determine annually and spatially averaged tolerance limits for coral reefs under current ocean conditions. New tolerance limits and the quantified potential reef habitats can allow us to predict the global reef distribution in the future under a changing climate. The potential coral-reef habitat area calculated with ReefHab is about $121 \times 10^3$ km$^2$ larger than the charted reefs. This indicates that the growth potential of coral reefs could be higher than currently observed in the absence
of other anthropogenic perturbations such as fishing, local damage, and pollution.
3 Global coral reef habitat suitability in response to ocean warming, acidification, and eutrophication

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Abstract

In recent years, coral reefs have experienced major declines due to global and local threats like global warming, ocean acidification, and eutrophication. In order to develop appropriate conservation and restoration strategies it is of crucial importance to identify the current ecological status of coral reefs and to evaluate the impacts that changing environmental conditions may have on corals. Using global data of coral reef occurrence as a proxy for their long-term adaptation to contextual environmental conditions, we identify here the performance window of corals on a global scale and in relation to four critical environmental conditions, sea surface temperature (SST), aragonite saturation state ($\Omega_{ar,s}$), and nitrate (NO$_3$) and phosphate (NO$_4$) concentrations. We further quantify the current status of coral reef communities in relation to their regional environmental optima and provide a quantitative overview of the expected changes in coral reef habitat suitability across the tropics for variations of +0.1°C in SST, -0.02 in $\Omega_{ar,s}$, +0.02 μmol L$^{-1}$ in NO$_3$, and +0.01 μmol L$^{-1}$ in NO$_4$. While many coral reefs habitats of Southeast Asia, the Great Caribbean, Western Indian Ocean, and the central Pacific, will be negatively affected by these environmental changes, we single out areas with potential improvements thus constituting temporary refugia. These regions are the Nansha Islands (the Spratly Islands), the Andaman and Nicobar Islands, the northern Red Sea, and the Turks and Caicos Islands. We also find that local threats, such as nutrient eutrophication, will affect the central and southern GBR, Persian Gulf, coast of Oman, Kenya, Tanzania, and islands of the Central Pacific (along 20°S).

3.1 Introduction

Coral reefs are among the most productive and diverse ecosystems on Earth and have enormous ecological, social, and economic importance (Moberg and Folke 1999; Cesar and Chong 2004). They support almost one third of the world’s marine fish species (Newton et al. 2007) and provide around 10% of the total fish consumed by humans (Pauly et al. 2002). The total economic annual net benefits of healthy coral reefs with tourism potential is estimated between 23,100 and 270,000 USD/m$^2$ (Burke et al. 2002). However, these ecosystems and the ecological services they provide are being degraded (Hughes 1994; Pandolfi et al. 2003; Cesar et al. 2003; Gardner et al. 2003; Aronson et al. 2004; Côté et al. 2005; Bruno and Selig 2007; Hughes et al. 2007; Bruno et al. 2009; De’ath et al. 2012; Graham et al. 2015; de Bakker et al. 2017) by various anthropogenic stressors, including global warming, ocean acidification, eutrophication, overfishing, etc. (Bruno et al. 2003, 2007; Selig et al. 2006; Donner et al. 2007;
Hoegh-Guldberg et al. 2007; Hughes et al. 2007; Carpenter et al. 2008; Eakin et al. 2010; Burke et al. 2011; De’ath et al. 2012; Randall et al. 2014). These global (ocean acidification and global warming) and local (nutrient enrichment) stressors can have negative effects on coral reef systems at both organism and ecosystem levels (Gattuso et al. 1998; Langdon et al. 2000; Koop et al. 2001; Leclercq et al. 2002; Bruno et al. 2003; Carricart-Ganivet 2004; Ohde and Hossain 2004; Marshall and Clode 2004; Voss and Richardson 2006; Marubini et al. 2008; Cooper et al. 2008; Silverman et al. 2009; Ries et al. 2010; Vermeij et al. 2010; De’ath and Fabricius 2010; Eakin et al. 2010; Maynard et al. 2011; Randall et al. 2014; Hughes et al. 2017, 2018a; Eyre et al. 2018) and can accelerate biodiversity loss, impair ecological functions, and compromise reef resilience to disturbances (Hughes et al. 2003, 2018b). It is therefore of crucial importance to identify the current ecological status of coral reefs and to evaluate the impacts that changes in environmental conditions will have on coral reefs, especially for developing appropriate conservation and restoration strategies.

Over the last decades, many studies have attempted to assess the current and future status of coral reefs in relation to natural and human threats at various spatial scales (Halpern et al. 2007, 2008; Selkoe et al. 2009; Burke et al. 2011; Bryant et al. 2012; Couce et al. 2012, 2013, van Hooidonk et al. 2013, 2014, 2016; Freeman et al. 2013; Descombes et al. 2015; Freeman 2015; Cinner et al. 2016). A classic example is represented by the vulnerability map of global reef ecosystems by the Reefs at Risk Project (Burke et al. 2011; Bryant et al. 2012). This project produced a threat index that combined destructive fishing, coastal development, watershed-based pollution, and marine-based pollution and damages. Another prominent study (Selkoe et al. 2009) estimated the cumulative human impacts on coral reef ecosystems of the northwestern Hawaiian Islands by using information of anthropogenic threats in combination with habitat maps and expert judgment on the vulnerability of different habitat types. The subjective opinions of experts are obviously relevant contributions (Kappel et al. 2011) in relation to the social and institutional conditions characterising the region of interest, especially when based on observational data or direct experience. However, bias may exist due to individual backgrounds and research focus areas or to a phenomenon called ‘shifting baseline’ in which an individual’s perception of the state of an ecosystem is based on recent experience rather than on a long-term, historical perspective (Pauly 1995; Knowlton and Jackson 2008). Expert opinions, therefore, provide a rather qualitative assessment of coral reef status instead of quantitative information.
Additionally, the vast majority of studies tend to focus on regions where coral degradation is expected, thus overlooking areas suitable for coral habitats or with potential positive developments, i.e. the “bright spots” (Cinner et al. 2016). For example, the response of coral assemblages in the Great Barrier Reef (GBR) to the heat waves of 2016 and 2017 produced severe bleaching in the northern part of the GBR but no substantial impacts were observed in the southern part, which probably even benefitted from warming (Hughes et al. 2018b). Quantitative approaches are thus needed aiming at assessing the status of coral reefs and at identifying areas where habitat may remain suitable for coral reefs even under changing environmental conditions. Physical and chemical conditions can be quantified with accuracy and robust methods can be developed to identify the habitat suitability range of ecological communities in relation to such conditions. Refugia and habitat suitability maps for tropical corals have been proposed by previous studies (Couce et al. 2013; Freeman et al. 2013; van Hooidonk et al. 2013, 2014; Cacciapaglia and van Woesik 2015; Descombes et al. 2015). However, these previous studies considered only two environmental factors: warming and ocean acidification.

Here, we present a quantitative method for calculating a habitat suitability index for coral reefs that is based on their current position within global and regional ranges of physical and chemical factors, which are: (1) sea surface temperature, SST, (2) aragonite saturation state, \( \Omega_{\text{arag}} \), (3) nitrate concentration, \( \text{NO}_3 \), and (4) phosphate concentration, \( \text{PO}_4 \). We assume that coral reefs have adapted to these environmental ranges over evolutionary time scales and that the conditions under which they occur in the modern ocean can provide relevant information about their physiological adaptations and limits. Given the difficulties of measuring the physiological and ecological performances of coral reefs on a global scale and in relation to a diverse array of environmental factors, also due to the broad varieties of species forming the coral communities, we use the global dataset of coral reef occurrence as a proxy for their long-term adaptation to contextual environmental conditions and for defining their habitat suitability ranges. We infer coral habitat suitability ranges from the number of coral reefs occurring at given environmental conditions. According to this approach, coral communities living near the limits of their habitat suitability ranges are more vulnerable than those living close to their optimum. We quantify coral reef habitat suitability with respect to each environmental variable individually. This approach separates local threats (e.g. nutrient eutrophication, which is potentially manageable with waste water treatment) from global threats (e.g. global warming and ocean acidification, which requires global solutions for decreasing greenhouse gas emissions). We further provide an overview about
the expected change of coral reef habitat suitability across the tropics in relation to changes in environmental conditions. We thus identify areas that under environmental change can 1) remain suitable habitats or even improve (temporary refugia), 2) become unsuitable habitats in relation to local stressors (eutrophication), 3) become unsuitable habitat in relation to global stressors (warming and acidification), and 4) become unsuitable habitat in relation to both local and global stressors (respectively eutrophication and warming and/or acidification).

3.2 Methods

3.2.1 Coral Reef data

Charted reef data were obtained from the Global Distribution of Coral Reefs 2010\textsuperscript{140–143}. The data were originally recorded as polygons in DBF format, with the majority (85\%) of them mapped at a 30 m resolution. We used this data to create an ‘observed’ reef habitat distribution map at a 30” × 30” grid cell resolution. Specifically, we overlaid the charted reef polygons onto a 21600 × 43200 matrix of the bathymetric profile (obtained from GEBCO_08 Grid, version 2010, available at http://www.gebco.net in netCDF format). Any grid cell that contained one or more points of a reef polygon was assigned the value of 1, reflecting the presence of coral reefs or a suitable reef habitat. The value 0 was assigned to grid cells that did not contain reefs.

3.2.2 Environmental data

We considered global data of temperature (T) (Locarnini et al. 2013), nitrate (NO\textsubscript{3}) (Garcia et al. 2014), phosphate (PO\textsubscript{4}) (Garcia et al. 2014), and aragonite saturation state (Ω\textsubscript{ara}) at the sea surface. Temperature data is provided on a spatial resolution of 0.25° × 0.25°, while nitrate and phosphate data are on a 1° × 1° spatial resolution. The aragonite saturation state (Ω\textsubscript{ara}) was calculated from alkalinity and dissolved inorganic carbon (DIC) data obtained from the Global Ocean Data Analysis Project (GLODAP) (Key et al. 2004) using the software CO2SYS (Lewis and Wallace 1998). Both DIC and alkalinity, have a 1° × 1° spatial resolution. We interpolated the areas that were not covered by the GLODAP dataset (e.g. the Indonesian Sea and the Caribbean). The interpolation algorithm is based on a penalized least squared method (Garcia 2010; Wang et al. 2012). We interpolated DIC and alkalinity, and then used these two interpolated datasets to calculate Ω\textsubscript{ara}. The resolution of all environmental data was adapted
to match the spatial resolution of the coral reef data (i.e. 30° × 30°). This was done by subdividing the 0.25° × 0.25° grid cells of T into 30 × 30 sub-grid cells and the 1° × 1° grid cells of NO₃, PO₄ and Ω₉₃ into 120 × 120 sub-grid cells. The sub-grid cells are assigned the same environmental conditions according to the value of the original cell subdivision.

3.2.3 Suitability index

We combined the observed spatial distribution of coral reefs with each environmental variable and analysed the frequency distribution of reef occurrence for each environmental variable at the global scale. We constructed histograms between the minimum and maximum of each environmental variable x at the corresponding charted coral reef location. The bin size of each histogram was determined by the Freedman–Diaconis’ rule (Freedman and Diaconis 1981) using the following formula:

\[
\text{Bin size} = 2 \left[ \frac{q_{75} - q_{25}}{3\sqrt{n}} \right]
\]

Where \( q_{75} - q_{25} \) is the interquartile range of the data and \( n \) is the number of observations of each environmental variable.

We then used a skewed normal distribution model to fit each histogram. The skewed normal distribution was chosen due to the hump-shaped relationship between each environmental variable and frequency distribution of reef occurrence showed in each histogram.

The standard normal probability density function \( \varphi(x) \) is defined as

\[
\varphi(x) = \frac{1}{\sqrt{2\pi}} e^{-\frac{x^2}{2}}
\]

The cumulative distribution function is defined as

\[
\Phi(x) = \int_{-\infty}^{x} \varphi(t)dt = \frac{1}{2} \left[ 1 + \text{erf} \left( \frac{x}{\sqrt{2}} \right) \right]
\]

Where \( \text{erf} \) is the error function, defined as

\[
\text{erf}(x) = \frac{2}{\sqrt{\pi}} \int_{0}^{x} e^{-t^2} dt
\]
The frequency distribution function of a skewed normal distribution is given by

$$F(x) = 2\varphi(x)\Phi(\alpha x)$$  \hspace{1cm} (4)

where the parameter $\alpha$ defines the skewness of the distribution. When $\alpha = 0$, the frequency distribution equals a normal distribution. The distribution is right skewed when $\alpha > 0$ and left skewed when $\alpha < 0$. The skewness increases as the absolute value of $\alpha$ increases.

By applying the transformation $x \rightarrow \frac{x-\xi}{\omega}$, we obtain:

$$F(x) = \frac{2}{\omega} \varphi \left( \frac{x-\xi}{\omega} \right) \Phi \left[ \alpha \left( \frac{x-\xi}{\omega} \right) \right]$$  \hspace{1cm} (5)

The statistical parameters $\xi$, $\alpha$, and $\omega$, represent, respectively, location, skew, and scale. We introduced a fourth parameter $\kappa$ representing the amplitude of $F(x)$, so that:

$$F(x) = \frac{2}{\omega} \varphi \left( \frac{x-\xi}{\omega} \right) \Phi \left[ \alpha \left( \frac{x-\xi}{\omega} \right) \right] \kappa$$  \hspace{1cm} (6)

The best values of the four statistical parameters were derived numerically by fitting the histograms iteratively, starting with initial guessed values and iterating until a minimum sum of the variation (chosen as less than 0.01) from the original data was obtained according to a least-square function. The best values for $\xi$, $\alpha$, $\omega$, and $\kappa$ are reported in Supporting Information Table B.1.

The fitted frequency distributions $F(x)$ were then normalized to the range 0 and 1 by scaling the function to the minimum and maximum values as follows

$$F(x)_n = \frac{F(x) - \min(F(x))}{\max(F(x)) - \min(F(x))}$$  \hspace{1cm} (7)

The value of the normalized frequency distribution $F(x)_n$ is 1 when reef occurrence is highest and is 0 when reef occurrence is lowest.

We assume that coral reefs have adapted to their environments over evolutionary time scales and that the conditions under which they thrive in the modern ocean can reflect the relevant habitat suitability, $S(x)_n$, for coral reefs.

Thus,
\[ S(x)_n = F(x)_n \times 100\% \]  \hspace{1cm} (8)

With \( S(x)_n = 100\% \) indicating an optimum condition (i.e. environmental values at which most of the reefs are found and thus suitable for coral growth) and the \( S(x)_n = 0\% \) indicating an unsuitable environmental condition (i.e. the condition least suitable for coral growth).

We also analysed the frequency distributions of reef occurrences for each environmental variable at a regional scale for six major regions (geographic information for the select regions are reported in Supporting Information Table B.2). Regional histograms and normalised frequency distributions of reef occurrences were obtained following the same procedure described above for the global case.

The number of reefs found in each region are reported in Supplementary Table S2. The six regions contained a total of 25,270 reefs, 85 % of the global reef cover (accounting for 29,550 reefs).

### 3.2.4 Habitat suitability change

We calculated derivatives of the regional habitat suitability to quantify the relative change in habitat suitability with respect to a bin size change in each environmental variable. These calculations provide the habitat suitability change with respect to a potential 0.1°C warming, 0.02 decrease in \( \Omega_{\text{ara}} \), 0.02 \( \mu \text{mol L}^{-1} \) increase in \( \text{NO}_3 \) concentration, or 0.01 \( \mu \text{mol L}^{-1} \) increase in \( \text{PO}_4 \) concentration (Supporting Information Figure B.1).

### 3.2.5 Reef habitat classification

Within the six regions, areas were classified as follows. Areas showing a positive habitat suitability change with respect to all four environmental variables were classified as temporary refugia. Areas sowing a negative habitat suitability change under warming and/or decrease in \( \Omega_{\text{ara}} \) were considered under global threats. Areas showing a negative habitat suitability change with respect to increase of nitrate and/or phosphate were considered under local threats. Finally, areas showing a negative habitat suitability change due to warming and/or decrease in \( \Omega_{\text{ara}} \) and increase in nitrate and/or phosphate were considered under global and local threats.
3.3 Results

Figure 3.1 shows the occurrences of coral reefs with respect to SST, $\Omega_{\text{ara}}$, NO$_3$, and PO$_4$ on a global scale, i.e. considering all coral reefs worldwide (for a total of 29,550 reefs, see Methods). The histograms (Figure 3.1, green bars) and frequency distributions (Figure 3.1, red lines) represent the range of environmental conditions under which reefs are currently found and are characterised by optima (i.e. the values of each environmental variable corresponding to the highest occurrence of coral reefs). The statistical parameters characterising the frequency distributions ($\xi$, $\alpha$, $\omega$, and $\kappa$ for location, skew, scale, and amplitude, respectively) are reported in Supporting Information Table B.1.

We assume that the environmental conditions under which the majority of reefs are found reflect the most suitable conditions (i.e. the optimal conditions) for coral reef growth. These optima, which are inferred from the frequency distributions, are 28.7°C, 3.8, 0.15 µmol L$^{-1}$, and 0.16 µmol L$^{-1}$ for, respectively, SST, $\Omega_{\text{ara}}$, NO$_3$, and PO$_4$ (Table 3.1).

**Figure 3.1** Histograms (green bars) of global reef occurrences and global normalized frequency distributions (red lines) in relation to different environmental variables. The bin sizes of the histograms for each variable are calculated using the Freedman-Diaconis’ rule (see Methods). The bin sizes for SST, $\Omega_{\text{ara}}$, NO$_3$, and PO$_4$ are 0.1°C, 0.02, 0.02 µmol L$^{-1}$,
and 0.01 μmol L⁻¹, respectively. The statistical parameters (ξ, α, and ω, and κ for, respectively, location, skew, scale, and amplitude) characterising the frequency distributions are reported in Supporting Information Table B.1.

**Table 3.1** Global and regional optima (i.e. environmental values corresponding to the highest number of coral reef occurrences) for different environmental variables.

<table>
<thead>
<tr>
<th>Variable</th>
<th>SST (°C)</th>
<th>Ω_{ara}</th>
<th>NO₃ (μmol L⁻¹)</th>
<th>PO₄ (μmol L⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Global</td>
<td>28.7</td>
<td>3.8</td>
<td>0.15</td>
<td>0.16</td>
</tr>
<tr>
<td>Southeast Asia</td>
<td>28.6</td>
<td>3.7</td>
<td>0.35</td>
<td>0.17</td>
</tr>
<tr>
<td>Great Barrier Reef</td>
<td>26.9</td>
<td>3.3</td>
<td>0.17</td>
<td>0.13</td>
</tr>
<tr>
<td>Great Caribbean Region</td>
<td>27.8</td>
<td>4.0</td>
<td>0.21</td>
<td>0.09</td>
</tr>
<tr>
<td>Red Sea &amp; Persian Gulf</td>
<td>29.4</td>
<td>4.0</td>
<td>0.21</td>
<td>0.12</td>
</tr>
<tr>
<td>Western Indian Ocean</td>
<td>27.5</td>
<td>3.8</td>
<td>0.04</td>
<td>0.17</td>
</tr>
<tr>
<td>Central Pacific</td>
<td>28.0</td>
<td>4.0</td>
<td>0.08</td>
<td>0.16</td>
</tr>
</tbody>
</table>

Since these frequency distributions represent an aggregation of multiple species over a global scale, they mask potential adaptations of coral communities to local environmental conditions. To identify regional differences, we computed reef distributions in specified regions of the tropical oceans. These regions contained a total of 25,270 reefs, 85% of the reefs found worldwide (see Methods). The statistical parameters of frequency distributions are reported in Supporting Information Table B.1.
Figure 3.2 Normalised frequency distributions of reef occurrences for the various environmental variables and for specific regions. The statistical parameters of the frequency distributions are reported in Supporting Information Table B.1. The vertical dashed lines mark the global environmental optima (Figure 3.1).

When the regional frequency distributions are compared and related to the global environmental optima, clear differences can be identified among regions (Figure 3.2). For example, the Great Barrier Reef (GBR) is the region with the lowest SST optimum, 26.9°C (Figure 3.2a and Table 3.1). In contrast, the Red Sea and Persian Gulf show the highest SST optimum, 29.4°C. The coral reefs of the Southeast Asia, GBR, the Western Indian Ocean, the Great Caribbean Region, and the Central Pacific region show SST optima that are lower than the global SST optimum (Table 3.1). The reefs of the GBR show the lowest $\Omega_{\text{ara}}$ optimum, while the reefs of the GBR and Southeast Asia exhibit $\Omega_{\text{ara}}$ optima that are lower than the global optimum. The $\Omega_{\text{ara}}$ Optimum of the Western Indian Ocean coincides with the global optimum. The optima of the Red Sea and Persian Gulf and the Great Caribbean are above the global optimum (Figure 3.2b and Table 3.1). Reefs of the Western Indian Ocean and Central Pacific show a NO$_3$ optimum that is lower than the global one. The reefs from all other regions have optima above the global one (Figure 3.2c and Table 1). Reefs of the GBR, Great Caribbean, and Red Sea and Persian Gulf show PO$_4$ optima that are well below the global value (Figure 3.2d and Table 1). All other regions have optima that are above the global optimum.
Environmental conditions at reef locations in combination with habitat suitability maps provide visual overviews about the current status of reef communities. In general, reef locations at relatively higher latitudes and several reef locations along the equator show lower habitat suitability in relation to SST (Figure 3a-b). Low habitat suitability in reef locations along the equator results from SST values above the corresponding regional optima, whereas low suitability at high latitudes is produced by SST values below the corresponding regional optima.

We quantified changes in habitat suitability with respect to warming by 0.1°C. In Southeast Asia (Figure 3.3c, box 1), the habitat suitability of reef locations along the equator will be low. However, habitat suitability in the Philippines, the Java Sea, and the Flores Sea will improve. In the GBR (Figure 3.3c, box 2), a latitudinal pattern of habitat suitability change emerges. The habitat suitability in the northern part of the GBR will decrease, while the habitat suitability in the central and southern parts of the GBR will increase. Cuba (Caribbean side), Coast Rica, and Panama (Figure 3.3c, box 3) show a decrease in habitat suitability. Habitat suitability in the Maldives decreases slightly (Figure 3.3c, box 5). The habitats of other regions, such as those in the Mozambique Channel (Figure 3.3c, box 5), the Red Sea and Persian Gulf (Figure 3.3c, box 4), and the Central Pacific (Figure 3.3c, box 6) remains relatively unchanged or will become slightly more suitable.
**Figure 3.3** SST at reef locations (a). Habitat suitability in per cent in relation to SST and specific to each region (b). Habitat suitability change with respect to warming by +0.1°C (c). The colours in habitat suitability change map (c) indicate the intensity of the change and the direction thereof. A more suitable habitat, indicated by blue, occurs when the change in SST moves towards the regional optimum; whereas a less suitable habitat, indicated by red, occurs when the change in SST moves away from the regional optimum.

Most reef habitats are found at relatively high $\Omega_{\text{ara}}$. However, the northern part of the GBR, Baja California, and the Galápagos Islands exhibit relatively low $\Omega_{\text{ara}}$ conditions, between 2.82 and 3.28 (Figure 3.4a). The lowest $\Omega_{\text{ara}}$ (on a global scale) is 2.82 and is found in Baja California (Guan et al. 2015). Thailand, Malaysia, West Sumatra (Figure 3.4b, box 1), the southern part of the GBR (Figure 3.4b, box 2), the western Great Caribbean Region (Figure 3.4b, box 3), the northern Red Sea and the coast of Oman (Figure 3.4b, box 4), the Maldives and the western Mozambique Channel (Figure 3.4b, box 5) show low habitat suitability with respect to their corresponding regional optima. A change in $\Omega_{\text{ara}}$ by -0.02 produces a decrease in habitat suitability in the Philippines, the Molucca Sea, and the Banda Sea (Figure 3.4c, box 1), the northern GBR (Figure 3.4c, box 2), the Great Caribbean Region (Figure 3.4c, box 3), the southern Mozambique Channel (Figure 3.4c, box 5), and the Solomon Islands, Vanuatu, and the new Caledonia (Figure 3.4c, box 6). The northern Red Sea (Figure 3.4c, box 4) shows a slightly increase in habitat suitability with respect to a 0.02 decrease in $\Omega_{\text{ara}}$. 
Figure 3.4 $\Omega_{ara}$ at reef locations (a). Habitat suitability in relation to $\Omega_{ara}$ and specific to each region (b). Habitat suitability change with respect to a change in $\Omega_{ara}$ by -0.02 (c). The colours in habitat suitability change map (c) indicate the intensity of the change and the direction thereof. A more suitable habitat, indicated by blue, occurs when the change in $\Omega_{ara}$ moves towards the regional optimum; whereas a less suitable habitat, indicated by red, occurs when the change in $\Omega_{ara}$ moves away from the regional optimum.

Coral reefs in Southeast Asia, the Caribbean Sea, the Galápagos Islands, the southern Red Sea, the coast of Oman, and islands in the Central Pacific occur at moderate to high NO$_3$ concentrations (Figure 3.5a). The Makassar Strait, Gulf of Thailand (Figure 3.5b, box 1), Cuba, Coast Rica and Panama (Figure 3.5b, box 3), the southern Red Sea and the coast of Oman (Figure 3.5b, box 4), the Seychelles, Kenya, and Tanzania (Figure 3.5b, box 5), and equatorial islands in the Central Pacific (Figure 3.5b, box 6) show low habitat suitability with respect to NO$_3$. An increase in NO$_3$ by 0.02 $\mu$mol L$^{-1}$ does not alter the habitat suitability of these regions (Figure 3.2c) because NO$_3$ in these regions is already well above the corresponding regional optima. An increase in NO$_3$ by 0.02 $\mu$mol L$^{-1}$ produces a decline in habitat suitability in the Southeast Asia (Figure 3.5c, box 2), the central and southern GBR (Figure 3.5c, box 2), the northern and central Red Sea and Persian Gulf (Figure 3.5c, box 4), the Western Indian Ocean (Figure 3.5c, box 5), and Marshall Islands and the islands of the Central Pacific between 10°S and
20°S (Figure 3.5c, box 6).

Figure 3.5 NO$_3$ concentrations at reef locations (a). (b) Habitat suitability in relation to NO$_3$ and specific to each region (b). Habitat suitability change with respect to a change in NO$_3$ concentration by +0.02 µmol L$^{-1}$ (c). The colours in habitat suitability change map (c) indicate the intensity of the change and the direction thereof. A more suitable habitat, indicated by blue, occurs when the change in NO$_3$ moves towards the regional optimum; whereas a less suitable habitat, indicated by red, occurs when the change in NO$_3$ moves away from the regional optimum.

Coral reefs in the Makassar Strait, the Strait of Malacca, the coast of Oman, the Galápagos Islands, and islands in the Central Pacific occur at moderate to high PO$_4$ concentrations (Figure 3.6a). The Makassar Strait (Figure 3.6b, box 1), the central outer GBR (Figure 3.6b, box 2), Panama and Costa Rica (Pacific side) and Venezuela (Figure 3.6b, box 3), the coast of Oman (Figure 3.6b, box 4), and islands in the Central Pacific along the equator (Figure 3.6b, box 6) show low suitability due to relatively high PO$_4$. An increase in PO$_4$ by 0.01 µmol L$^{-1}$ decreases habitat suitability in the Southeast Asia (Figure 3.6c, box 1), the Caribbean Sea (Figure 3.6c, box3), Seychelles, Maldives, Kenya, and Tanzania (Figure 3.6c, box 5), islands in the Central Pacific, between 10° S and 20°S (Figure 3.6c, box 6). In contrast, the habitat suitability of the inner GBR (Figure 3.6c, box 2), the Bahamas (Figure 3.6b, box 3), Marshall Islands and islands in the Central Pacific along 20°S (Figure 3.6c, box 6) increases as PO$_4$ increases because
these reefs are below their regional optimum (Figure 3.6c, box 5).

![Figure 3.6 PO₄ concentrations at reef locations (a), (b) Habitat suitability in relation to PO₄ and specific to each region (b). Habitat suitability change with respect to an increase in PO₄ concentrations by 0.01 µmol L⁻¹ (c). The colours in habitat suitability change map (c) indicate the intensity of the change and the direction thereof. A more suitable habitat, indicated by blue, occurs when the change in PO₄ moves towards the regional optimum; whereas a less suitable habitat, indicated by red, occurs when the change in PO₄ moves away from the regional optimum.]

The results of habitat suitability change with respect to 0.1°C warming, -0.02 change in Ω₃₉₃, 0.02 µmol L⁻¹ increase in NO₃, and 0.01 µmol L⁻¹ increase in PO₄, can be used to classify coral reef locations into four major categories: (1) temporary refugia, if regional conditions in all four environmental variables change towards the corresponding optima, (2) local threat, if regional conditions in NO₃ and/or PO₄ concentrations shift away from the corresponding optima, (3) global threat, if regional conditions in SST and/or Ω₃₉₃ shift away from the corresponding optima, or (4) global and local threats, if regional conditions in SST and/or Ω₃₉₃ and NO₃ and/or PO₄ shift away from corresponding optima.

This classification shows that reef locations with local threat (i.e. under a 0.02 µmol L⁻¹ increase in NO₃ and/or 0.01 µmol L⁻¹ increase in PO₄) will be mainly found in the central and southern GBR, Persian Gulf, coast of Oman, Kenya,
Tanzania, and islands of the Central Pacific (along 20°S). They account for about 26% of the locations covered by corals in all six regions. Areas with global threat (i.e. under a 0.1°C warming and/or a 0.02 reduction in $\Omega_{\text{ara}}$) will be mainly found in the Philippines, northern GBR, and New Caledonia and account for 17% the reefs locations covered by the six regions. Areas with both local and global threats will be found in all six regions, especially in Southeast Asia, the Great Caribbean, Western Indian Ocean, and in the Central Pacific, accounting for about 54% of the reef locations covered by the six regions. Temporary refugia will be the Nansha Islands (the Spratly Islands), the Andaman and Nicobar Islands, northern Red Sea, and the Turks and Caicos Islands. They account for only 3% of the reef locations covered by the six regions.

![Classification of coral reef habitat locations](image)

**Figure 3.7** Classification of coral reef habitat locations with respect to an increase in SST by 0.1°C, a decrease in $\Omega_{\text{ara}}$ by 0.02, an increase in NO$_3$ by 0.02 μmol L$^{-1}$, or an increase in PO$_4$ by 0.01 μmol L$^{-1}$. Temporary refugia (green), only 3% of the reefs in the six regions, are locations in which these changes in environmental conditions will maintain or increase habitat suitability. Locations that will face a decline in habitat suitability due to increase in NO$_3$ and/or PO$_4$ are classified as local threat (blue) and cover 26% of the reefs in the six regions. Locations that will face a negative habitat suitability change with respect to warming and/or decreasing $\Omega_{\text{ara}}$ are classified as global threat (yellow), 17% of the reefs in the six regions. Locations that will face a decrease in habitat suitability due to warming and/or decreasing $\Omega_{\text{ara}}$ and increase in nitrate and/or phosphate are classified as global and local threats (red), 54% of the reefs in the six regions.

### 3.4 Discussion

In the present study, we assumed that coral reefs have adapted to their environments over evolutionary time scales and that the conditions under which they thrive in the modern ocean reflect suitable habitats. We analysed global and regional reef occurrences with respect to different environmental variables in order to develop a suitability index for coral reef habitats.
The global frequency distributions of coral reef occurrence (Figure 3.1) show that optimal environmental conditions for corals are characterized by 28.7°C, 3.8, 0.15 μmol L⁻¹, 0.16 μmol L⁻¹ for SST, Ω₉₀, NO₃, and PO₄. The SST optimum is consistent with results from physiological experiments, indicating that the optimal temperature for coral growth is between 28 and 29°C (Sawall et al. 2015). The shapes of the global distributions for nitrate and phosphate are also in agreement with a conceptual model of coral physiology suggesting that the performance of these organisms can be sub-optimal at very low nutrient concentrations and that they can benefit from slight nutrient enrichments (D’Angelo and Wiedenmann 2014).

The regional frequency distributions (Figure 3.2) show clearly that coral communities of different regions are adapted to distinct environmental conditions. For example, the thermal optimum for corals in the GBR is almost 2°C lower than the global optimum, while the Red Sea and Persian Gulf are characterized by a regional thermal optimum that is almost 1°C higher than the global optimum (Figure 3.2a). Large-scale bleaching events that occurred in the GBR and in the Caribbean over the last decades (Berkelmans and Oliver 1998; McWilliams et al. 2005; Eakin et al. 2010; Hughes et al. 2017) suggest clearly that despite being located below the global SST optimum, the coral reef communities of these regions are close to their physiological limits due to adaptations to local conditions. Nonetheless, our analysis suggests that high temperature-adapted corals of the Red Sea and Persian Gulf could, in theory, be transplanted in the GBR and do well in a future warmer ocean. However, our results also show that coral communities adapted to high temperatures (e.g. those of the Red Sea and Persian Gulf) are also adapted to high Ω₉₀ (Figure 3.2). Therefore, corals from the Red Sea and Persian Gulf may face difficulties in the GBR because of the lower Ω₉₀ conditions there. In addition, it has been shown that increasing pCO₂ reduces the temperature threshold for coral bleaching (Anthony et al. 2008), which may counteract the ability of high temperature-adapted corals to survive in the GBR under warming conditions. The regional frequency distributions with respect to nutrient concentrations complicates the general picture. Corals in the Western Indian Ocean are, for example, adapted to a relatively low N:P ratio (about 0.5), while corals in the Caribbean are adapted to a higher N:P ratio (about 5.3). Thus, the success of coral transplants from region to region may also depend on the N:P ratio, an additional factor that can alter the susceptibility of corals to bleaching (Wooldridge 2009a; Wiedenmann et al. 2013; D’Angelo and Wiedenmann 2014; Pogoreutz et al. 2017).

Our results also reveal large spatial variability in habitat suitability and habitat suitability change when temperature increases by 0.1°C with strongest reduction
of habitat suitability in equatorial Southeast Asia (Figure 3.3). This is consistent with previous studies reporting a low habitat suitability in Southeast Asia (Couce et al. 2013) and the identification of this region as a hotspot for future coral bleaching (van Hooidonk et al. 2013, 2014). It has been suggested (Darling et al. 2012) that ocean warming can lead to alteration of coral communities via shifts towards more competitive, weedy, stress-tolerant taxa. We therefore expect that in this region ocean warming will produce changes in community compositions (Loya et al. 2001; McClanahan et al. 2007; McClanahan and Muthiga 2014; Baumann et al. 2016) and biodiversity loss (Munday et al. 2008; Descombes et al. 2015; Holbrook et al. 2015). Coral reef of the Southeast Asian region should therefore be a priority for conservation.

Coral reef locations characterised by temperatures below the regional optimum, will become more suitable with a +0.1°C change in temperature (Figure 3.3c). This is consistent with previous studies (van Hooidonk et al. 2013) suggesting that temporary refugia for coral reefs include the Western Indian Ocean, Thailand, southern GBR, and central French Polynesia. An increase in habitat suitability in relation to SST is confirmed, for example, by studies on massive Porites conducted on reefs of the southeast Indian Ocean, off Western Australia (Cooper et al. 2012), where increasing calcification rates with increasing temperature observed on the high-latitude reefs contrasted with declining coral trends reported on portions of the GBR (Cooper et al. 2008). Our results confirm these latitudinal differences, with the northern GBR showing a decrease in habitat suitability and the southern GBR showing an increases in habitat suitability under a 0.1°C warming (Figure 3.3c).

The exact functional dependence of coral reefs on $\Omega_{ara}$ is not clearly determined due to the contrasting results obtained from physiological (Gattuso et al. 1998; Ohde and Hossain 2004; Marubini et al. 2008; Ries et al. 2010) and ecological experiments (Langdon et al. 2000; Leclercq et al. 2002). The differences in regional frequency distributions found in our study may reflect a high species-specific variability in the way corals are adapted to $\Omega_{ara}$. For example, the habitat suitability index in the GBR shows an apparently inconsistent pattern (Figure 3.4b, box 2), with higher habitat suitability where $\Omega_{ara}$ is relatively low and lower habitat suitability where $\Omega_{ara}$ is relatively high. This is because, according to our method, a high habitat suitability is obtained in locations with a high number of reef occurrences and most reef locations in the GBR are found in the northern part, which is characterised by lowest $\Omega_{ara}$ values (Figure 3.4a), below about 3.45 (Supporting Information Figure B.2). A decline in $\Omega_{ara}$ by 0.02 in the GBR is thus mainly associated to an increase in habitat suitability change in central and southern GBR (Figure 3.4c) because this change depends on the regional
optimum, which is lower than most $\Omega_{\text{ara}}$ values in the region (Supporting Information Figure B.2).

The tropical eastern Pacific (Manzello et al. 2008), the coast of Oman (Burt et al. 2016), and the southern Mozambique Channel (Perry 2003) show a low $\Omega_{\text{ara}}$ suitability (Figure 3.4b). These reefs exhibit limited net carbonate production (Perry 2003; Manzello et al. 2008). However, a 0.02 reduction in $\Omega_{\text{ara}}$ does not produce a strong decline in habitat suitability (except for southern Mozambique, Figure 3.4c). Corals in locations characterised by water temperature below the thermal optima are more likely to withstand increasing pCO$_2$ (Reynaud et al. 2003; Silverman et al. 2009). However, areas that will be affected by both warming and decreasing $\Omega_{\text{ara}}$ will likely experience negative synergistic effects from these two stressors (Anthony et al. 2008, 2011; Prada et al. 2017). These areas are found in northern Sulawesi, Nusa Tenggara Timur, Solomon Islands, Marshall Islands, the Caribbean Sea, and the Pacific sides of Costa Rica and Panama (Figure 3.3c & Figure 3.4c & Supporting Information Figure B.3).

Many locations show low habitat suitability due to of relatively high nutrient concentrations. Most of these locations, like for example the coast of Oman (Figure 3.5 & 6 box 4), the equatorial portion of the Central Pacific (Figure 3.5 & 6 box 6), and the Pacific side of Coast Rica and Panama (Figure 3.5 & 6 box 3), are typically influenced by upwelling. The central Caribbean region and the equatorial reefs in Indonesia and Thailand, also show low habitat suitability due to relatively high nutrient concentrations, which are likely due to anthropogenic influences, including enhanced use of fertilizers and other land-use practices (Shulman and Robertson 1996) and wastewater pollution associated with coastal development (Chou et al. 2002). Increasing nutrient concentrations, by 0.02 μmol L$^{-1}$ for nitrate or by 0.01 μmol L$^{-1}$ for phosphate, produce significant declines in habitat suitability in Indonesia, the GBR, the Caribbean, the Maldives, and the central Pacific (for islands along 10 °N and between 10 °S and 20 °S, Figure 3.5c and Figure 3.6c). These reefs currently occur under optimal nutrient conditions (indicated by a high habitat suitability in relation to nutrient, Figure 3.5b & 3.6b) but are nonetheless very close to the threshold value at which the frequency of reef occurrences drastically declines (Figure 2c & 2d, Supporting Information Figure B.1).

Our analysis indicates the presence of locations with positive habitat suitability change under changing environmental conditions (+0.1°C, -0.02, +0.02 μmol L$^{-1}$, and +0.01 μmol L$^{-1}$ for, respectively, SST, $\Omega_{\text{ara}}$, NO$_3$, and PO$_4$). These locations could act as temporary refugia for coral reefs, account for only 3% of the total number of reefs in the six regions and are found in the Nansha Islands (the
Spratly Islands), the Andaman and Nicobar Islands, northern Red Sea, and the Turks and Caicos Islands (Figure 3.7).

A recent study suggested northern Indonesia as coral refugia under the condition that the current climate will be maintained until the year 2100 (Cacciapaglia and van Woesik 2015). Our results show that northern Indonesia is characterised by relatively high temperatures both regionally (Figure 3.2a) and globally (Figure 3.3a). This indicates that SST in northern Indonesia can easily exceed the global and regional thermal optima (respectively, 28.7°C and 28.6°C) under global warming. Thus, northern Indonesia will most likely be a bleaching hotspot in the near future (Donner et al. 2005; van Hooidonk et al. 2013, 2014). In addition, northern Indonesia is affected by relatively high nutrient levels (Figure 3.3c and 4c), which makes it more unlikely for this region to be a coral refugia. Overall, we find that 17% of the total number of reefs in the six regions will experience a decline in habitat suitability under a 0.1°C increase and/or a 0.02 reduction in Ωref. These reefs are mainly located around the Philippines, northern GBR, and New Caledonia.

We find that about 26% of total number of reefs in the six regions will experience negative habitat suitability changes under increasing nutrient concentrations (Figure 3.7). Local wastewater management is the only way to prevent further reef degradation by nutrient eutrophication. Studies show that reducing local nutrient loads can delay reef loss for about a decade under the “business-as-usual” CO2 emission scenario (Kennedy et al. 2013). By protecting coral reefs from further deterioration, local conservation management programmes can potentially increase areas classifiable as temporary refugia to 29% of the total number of reefs in the six regions, thus buying humanity additional time for producing solutions against global threats such as warming and ocean acidification. Locations that will be affected by local threats should therefore be priority areas for conservation and restoration programmes.

About 54% of the total number of reefs in the six regions will likely be affected by both local and global threats under changing environmental conditions. These areas are located mainly in Southeast Asia, the Great Caribbean and central Pacific (Figure 3.7). In a recent global study, coral reefs were classified as “dark spots” or “bright spots” depending on whether the observed reef fish biomass fell below or raised above given thresholds (Cinner et al. 2016). Dark spots were found among coral reefs of Mauritius, Kenya, Tanzania, Seychelles, northern Madagascar, Jamaica, and Venezuela (Cinner et al. 2016). These dark spots fall into our categories of reefs in locations under local and/or global threats (Figure 3.7) under changing environmental conditions. These locations are good
candidates for MPAs and active restoration programmes. However, local management programmes may produce little benefits in areas subject to global threats because the impacts of warming and ocean acidification may outweigh the benefits from local management (Darling et al. 2010; Hughes et al. 2017).

In summary, our work forecasts potential coral reef habitat suitability change under warming, ocean acidification, and eutrophication. Our results suggest that a rise in SST by 0.1°C may improve habitat suitability at relatively higher latitudes but about 17% of reef locations in the six regions will experience a decline in habitat suitability under warming by 0.1°C and/or a decline in Ωarα by 0.02. About one fourth of the reefs in the six regions will be under local threats, if nitrate and/or phosphate will increase by 0.02 µmol L⁻¹ and 0.01 µmol L⁻¹, respectively. While only 3% of reef locations in the six regions will constitute temporary refugia, more than half of reef locations in the six regions will be affected by both global and local threats under changing environmental conditions. For such areas, combining local management with the reduction of greenhouse gasses remains.
4 Predicting coral reef habitat suitability and potential coral reef habitats under global warming and ocean acidification

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Abstract

Rising atmospheric CO₂ concentrations cause warmer sea surface temperatures and ocean acidification, two global stressors that threaten coral reefs worldwide. The impacts of ocean warming and acidification on coral reefs are, however, spatially divergent. Here we present how these two processes alter potential reef habitats and habitat suitability based on the global response curve of coral reefs to temperature and aragonite saturation state. Future projections of sea surface temperature (SST) and aragonite saturation state (Ωₐra) are taken from ensembles of IPCC AR5 climate models using the new Representative Concentration Pathway (RCP) experiments and are used to extrapolate potential reef habitat and habitat suitability in current reef locations into the future. Using the highest CO₂ emission scenario RCP8.5 we find: (1) a poleward expansion of potential reef habitats towards higher latitudes due to warming; (2) the poleward expansion will be limited by acidifying polar waters; (3) the area of potential reef habitats will decline to half of its 2010 area in 2050; (4) the Great Barrier Reef, the Great Caribbean Region, and high latitude reef locations including Japan, Hawaii, the northern Red Sea, Persian Gulf, southern Madagascar, and Mauritius could serve as temporary refugia under ocean warming; (5) however, by the year 2100, ocean acidification will restrict reef accretion and result in no suitable reef habitat. Immediate global action to cut down CO₂ emission is essential to secure a better future for coral reefs.

4.1 Introduction

Accumulation of green house gases in the atmosphere (primarily carbon dioxide, CO₂), due to excessive burning of fossil fuel and land use change, has driven the average global temperatures to rise 0.8°C since preindustrial times (Hoegh-Guldberg et al. 2007). The average ocean surface temperature is predicted to increase relative to preindustrial levels by 1.2°C to 3.2°C until the year 2100 depending on CO₂ emissions (Gattuso et al. 2015). Increasing ocean temperature and extreme ocean warming events (e.g. heat waves, El Nino) often induce mass coral bleaching events (e.g. Glynn 1991; Berkelmans and Oliver 1999; Hughes et al. 2018). It is predicted that under CO₂ emissions scenario RCP8.5, 26% of coral reefs will experience annual bleaching events beginning in the year 2035 (van Hooidonk et al. 2014). Bleached corals may not have enough time to recover prior to the following bleaching event and prolonged bleaching will lead to coral mortality. In contrast, warming has the potential to cause a poleward expansion of reef corals that were previously limited by low temperatures (Thomson 2010; Yamano et al. 2011; Baird et al. 2012; Tuckett et al. 2017). Corals play a
fundamental role in reef formation, and coral reefs serve as habitat for numerous other species (Knowlton et al. 2010). Thus, coral bleaching and mortality due to high temperature and poleward range expansions due to warming could both cause fundamental modifications of tropical and temperate ecosystems.

About one forth of the anthropogenically emitted CO\textsubscript{2} dissolves into the ocean (Sabine et al. 2004; Le Quéré et al. 2018). Absorption of excess CO\textsubscript{2} lowers seawater pH and changes the composition of carbonate species of seawater, resulting in a reduction of the carbonate ion (CO\textsubscript{3}\textsuperscript{2-}) concentration. This phenomenon is known as ocean acidification (OA) and it threatens marine calcifiers by reducing the saturation state for building their carbonate skeletons, leading to reduced calcification rate and growth (Cohen and Holcomb 2009; Comeau et al. 2013b; Peck et al. 2018). Although the coral calcification site is separated from seawater by at least two single-cell-thick epithelial layers, experimental and field studies have shown that decreased aragonite saturation (\(\Omega_{ara}\)) in the seawater results in reduced coral calcification (Gattuso et al. 1998; Langdon et al. 2000; Leclercq et al. 2002; Ohde and Hossain 2004; Marubini et al. 2008; Ries et al. 2010; Mollica et al. 2018). In addition, ocean acidification can also increase the rate of CaCO\textsubscript{3} sediment dissolution (Andersson et al. 2009; Silverman et al. 2009; Eyre et al. 2014) and bioerosion (Andersson and Gledhill 2013). Coral reefs persist in a balance of CaCO\textsubscript{3} production, dissolution, and bioerosion. Declining CaCO\textsubscript{3} production together with enhanced dissolution and bioerosion in coral reefs raise concerns that reefs will transfer from net accretion to net dissolution of CaCO\textsubscript{3}.

Coral reefs are sensitive to changing temperatures and ocean pH. The impacts of warming and OA will not occur uniformly in space and time across the global coral reef habitat (Pandolfi et al. 2011; Couce et al. 2013; Freeman et al. 2013; van Hooidonk et al. 2014). However, warming can provide new opportunities for corals to colonize new areas at high latitude due to removal of thermal constraints (Yamano et al. 2011; Tuckett et al. 2017). Nevertheless, as atmospheric CO\textsubscript{2} continues to rise, the pH at high latitude waters will drop by more than 0.2 (Cao and Caldeira 2008), presumably resulting in a limiting effect on the poleward shift of coral reefs. Therefore, it is important to understand the possible response of coral reefs to combined warming and OA and to estimate how coral reefs will be distributed in the ocean under future climate change scenarios. Conservation and restoration actions, such as establishing protected areas (MPAs) or no-take zones, rearing and transplanting of coral reef fragments all require future prospects of how coral reefs will respond.
Species distribution modelling (SDM) represents ideal tools for predicting the species’ response and distribution. One of the most commonly used SDMs to predict coral reef distributions is Maxent (Couce et al. 2012, 2013; Freeman et al. 2013; Freeman 2015). Maxent is calibrated with species presence-only data. It estimates the species probability distribution that has maximum entropy (i.e. that is most spread out, or closest to uniform), subject to a set of constraints based upon the environmental conditions at known occurrence sites (Phillips et al. 2004; Phillips and Dudík 2008). In spite of the popularity (Renner and Warton 2013) and its outperformance over other methods (Elith et al. 2006), Maxent has difficulties in projecting species distributions into novel conditions that are outside of those used to calibrate the model. Maxent commonly treats variables outside the known range from samples as if they were at the limit of the known range (Phillips 2008). This effect makes the response to be constant when extrapolating to novel conditions (Phillips 2008). However, studies show that corals cannot tolerate extreme environmental conditions (e.g. high temperature, hypersaline, high light). Using a constant response to novel conditions will therefore contradict our biological knowledge.

In this study, we analyse the global coral reef occurrences along environmental variables in order to get the full suitability response curves and tolerance limits of coral reefs. By increasing the spatial scale of the studied area and then downscaled in its application (Pearson et al. 2002; Thuiller et al. 2004), we overcome the extrapolation difficulties. We assess global patterns of habitat suitability change within current coral reef habitats and range shifts of potential coral reef habitat under stress of ocean warming and acidification at a spatial scale of 30” × 30”. We assume that coral reefs have adapted to these environmental ranges over evolutionary time scales and that the conditions under which they occur in the modern ocean can provide relevant information about their physiological adaptations and limits. We then used our suitability response curves and tolerance limits to forecast future coral reef habitat suitability and potential habitat with respect to ocean warming and ocean acidification according to the RCP8.5 emission scenario (van Hooidonk et al. 2014).

4.2 Methods

4.2.1 Coral Reef data

The coral reef location data are obtained from the Global Distribution of Coral Reefs 2010. The original data are remapped onto a 30” × 30” grid cell
resolution. Specifically, the recorded reef polygons in the original data was overlaid onto a 21600 x 43200 matrix. Any grid cell that contained one or more points of a reef polygon was assigned the value of 1, reflecting the presence of coral reefs or a suitable reef habitat. The value 0 was assigned to grid cells that did not contain reefs.

4.2.2 Future projections of monthly SST and Ω_{ara} data

Ensembles of climate models for future projections of monthly mean sea surface temperature (SST) and Ω_{ara} under emission scenario RCP8.5 are taken from van Hooidonk et al. (2014) (downloaded from [http://onesharedocean.org/public_store/oo_aragonite/download.html](http://onesharedocean.org/public_store/oo_aragonite/download.html)). The time spans of ensemble data of SST and Ω_{ara} are from January 2006 to December 2090. The monthly mean SST and Ω_{ara} data were then used to calculate the annual mean SST and Ω_{ara}. The data of SST and Ω_{ara} both are at a 1° x 1° grid cell resolution.

4.2.3 Potential reef habitat

The annual mean thermal tolerance limits of global coral reefs are taken from Guan et al. (2015). The thermal tolerance limits are between 21.7°C and 29.6°C (Guan et al. 2015). The lower tolerance limit of Ω_{ara} is 2.82 (Guan et al. 2015). The tolerance limits are used to define the potential reef habitat. Areas that have SST and Ω_{ara} both within the tolerance limits are categorized as suitable reef habitats, while areas with SST and/or Ω_{ara} out of the tolerance limits are not suitable for coral reefs.

4.2.4 Reef habitat suitability response function

Reef habitat suitability response function is calculated as fitting a skewed normal distribution for the relationship between SST and Ω_{ara} and global frequency distribution of reef occurrence (more details in chapter 3). The skewed normal distribution is given by

\[ F(x) = \frac{2}{\omega} \varphi \left( \frac{x - \xi}{\omega} \right) \Phi \left( \alpha \left( \frac{x - \xi}{\omega} \right) \right) \kappa \]

where \( \varphi(x) \) is the standard normal probability density function and \( \Phi(x) \) is the cumulative distribution function. The parameter \( \alpha \) defines the skewness of the distribution, the statistical parameters \( \xi, \alpha, \omega, \) and \( \kappa \) represent, respectively,
location, skew, scale, and amplitude. The best values for $\xi, \alpha, \omega, \text{ and } \kappa$ are reported in Table 4.1. The symbol $x$ in the equation represents values of either SST or $\Omega_{ara}$.

Table 4.1 Statistical parameters $\xi, \alpha, \omega, \text{ and } \kappa$ (representing, respectively, location, skew, scale, and amplitude) for global fitted frequency distributions in relation to SST and $\Omega_{ara}$.

<table>
<thead>
<tr>
<th>Variable</th>
<th>$\xi$</th>
<th>$\alpha$</th>
<th>$\omega$</th>
<th>$\kappa$</th>
</tr>
</thead>
<tbody>
<tr>
<td>SST</td>
<td>29.27</td>
<td>-5.03</td>
<td>1.66</td>
<td>1.59</td>
</tr>
<tr>
<td>$\Omega_{ara}$</td>
<td>3.83</td>
<td>1.66x10^-3</td>
<td>0.21</td>
<td>0.20</td>
</tr>
</tbody>
</table>

The fitted frequency distributions $F(x)$ were then normalized to the range 0 and 1 ($F_n(x)$) by scaling the function to the minimum and maximum values as follows

$$F_n(x) = \frac{F(x) - \min(F(x))}{\max(F(x)) - \min(F(x))}$$

The value of the normalized frequency distribution $F_n(x)$ is 1 when reef occurrence is highest and is 0 when reef occurrence is lowest.

We assume that coral reefs have adapted to their environments over evolutionary time scales and that the conditions under which they thrive in the modern ocean can reflect the relevant habitat suitability, $S(x)$, for coral reefs.

Thus,

$$S(x) = F_n(x) \times 100\%$$

With $S(x) = 100\%$ indicating an optimum condition (i.e. environmental values at which most of the reefs are found and thus suitable for coral growth) and the $S(x) = 0\%$ indicating an unsuitable environmental condition (i.e. the condition least suitable for coral growth). The optimum condition for SST and $\Omega_{ara}$ were at 28.7°C and 3.8 (more details in chapter 3).
4.3 Results

We calculated the change in potential reef habitat distributions according to an ocean warming scenario of RCP8.5. In terms of SST, the area of potential reef habitats (i.e. areas that show SST within the thermal tolerance limits from 21.7°C to 29.6°C) decreases, particularly in the tropical region (Figure 4.1). The potential reef habitat with respect to SST in Southeast Asia starts to decrease from 2010, especially in equatorial areas (Figure 4.1). By 2090, areas between 20°N–20°S will no longer be able to serve as potential reef habitats due to an SST that is warmer than the upper thermal limit found in contemporary coral reefs (i.e. 29.6°C) (Figure 4.1 & Supporting Information Figure C.1). In contrast, the potential reef habitats with respect to SST have small ranges of poleward expansion in the shallow ocean areas around Japan, southern Australia, and the Mediterranean Sea (Figure 4.1 & Supporting Information Figure C.2). However, the poleward expansion is much smaller than the potential habitat loss in warm waters, leading to a net decline in the potential reef habitat with respect to SST.

With respect to the expected change in Ωara due to ocean acidification, the area of potential reef habitats (i.e. areas that show Ωara above the lower tolerance of 2.82) decline drastically (Figure 4.2). Figure 4.2 depicts a decrease in potential reef habitats with respect to Ωara towards the equator since 2010. By 2090, only small areas in the Caribbean and the central Red Sea are still potential reef habitats with respect to Ωara (Figure 4.2 & Supporting Information Figure C.3).

Subject to the combined impact of warming and acidification, the areas of potential reef habitats (i.e. areas that show SST and Ωara are both within the tolerance limits) decrease drastically (Figure 4.3). The poleward shifts of potential habitats due to warming are limited by decreasing Ωara (Figure 4.3 & Supporting Information Figure C.2). In 2050, areas in Southeast Asia will no longer be able to serve as potential reef habitats due to both SST and Ωara are out of the coral reef tolerance limits. However, the areas in the GBR, the Great Caribbean, the Red Sea and Persian Gulf are still potential reef habitats in 2050 (Figure 4.3).

The global area for potential reef habitats is projected to decline (Figure 4.4, black line). In 2050, the global potential reef habitat decreases to half of its 2010 area and disappear until 2100 (Figure 4.4, black line). In Southeast Asia, potential reef habitats will be affected earlier due to severe warming and ocean acidification (Figure 4.4, yellow line); whereas areas like the Red Sea and Persian Gulf as well as the Great Caribbean will be affected much later (Figure 4.4). Note
that these estimations are based on the global thermal and $\Omega_{ara}$ tolerance limits and that regional species may still suffer from warming and ocean acidification.

The coral reef tolerance limits with respect to SST and $\Omega_{ara}$ can define the range of potential reef habitat. Within the tolerance limits, corals can perform best under the optimal thermal and $\Omega_{ara}$ conditions, however, coral performance decreases under suboptimal conditions. The habitat suitability response function in this chapter defines the status of coral reefs with respect to SST and $\Omega_{ara}$. The colours of the reef locations as indicated by the colour dots in the figures (Figure 4.1 & Figure 4.2) indicate that within the tolerance limits with respect to SST and $\Omega_{ara}$ respectively, the habitat suitability is not uniformly distributed. Reef locations indicated by red dots are where conditions are close to the tolerance limits (i.e. lower or upper tolerance limit), indicate that these areas are already with lower suitability than the reef locations indicated by blue dots where conditions are close to optima. Within the thermal tolerance limits, there is spatial variability in the projected reef habitat suitability. Habitat suitability with respect to SST in Southeast Asia, the Central Pacific, the Maldives, the Comoro Islands, the Glorieuses, and the Seychelles decreases due to warming, moreover, the contemporary reef habitats in these regions are no longer suitable habitats by 2090 (Figure 4.1). However, habitat suitability with respect to SST in the Great Barrier Reef (GBR), the Great Caribbean region (with the exception of the Cayman Islands and Jamaica), and higher latitude reefs, such as those in ocean areas of Japan, Hawaii, the Persian Gulf, northern Madagascar, and Mauritius, increases due to warming (Figure 4.1). Note that the low habitat suitability with respect to SST in the GBR, the Great Caribbean, and high latitude reefs, such as those in Japan, Hawaii, the northern Red Sea, and Persian Gulf, in 2010 is due to the lower than optimal temperature (i.e. 28.64°C) (more details in chapter 3).

In Southeast Asia, the GBR, the Western Indian Ocean, and the Central Pacific, the habitat suitability with respect to $\Omega_{ara}$ decreases from 2010 onward (Figure 4.2). However, the habitat suitability with respect to $\Omega_{ara}$ in the Great Caribbean remains unchanged until 2020, at which point it decreases (Figure 4.2). In the Red Sea and Persian Gulf, the habitat suitability with respect to $\Omega_{ara}$ initially increases until 2040, at which point it begins to decrease (Figure 4.2). The increasing suitability is due to $\Omega_{ara}$ in the Red Sea and Persian Gulf are higher than the optimal of 3.8, ocean acidification thus push $\Omega_{ara}$ levels to the optima.

The projected global mean habitat suitability with respect to SST decreases relative to the global mean habitat suitability in 2010 (Figure 4.5a, black line). The mean habitat suitability with respect to SST decreases drastically in Southeast Asia; whereas it increases in the Great Caribbean region relative to the
mean habitat suitability in 2010 (Figure 4.5a). Other regions like the GBR, the Red Sea and Persian Gulf, and the Central Pacific show a relatively constant habitat suitability overall compare to the globally mean habitat suitability. This gives hope that the expected change in coral communities may not be so fatal and that an exchange of species can still maintain the coral reef structure over time.

The predicted habitat suitability with respect to $\Omega_{ara}$ are, however, more worrisome. The projected global mean habitat suitability with respect to $\Omega_{ara}$ decreases relative to the global mean habitat suitability in 2010 (Figure 4.5b). In Southeast Asia, the GBR, the Western Indian Ocean, and the Central Pacific, the mean habitat suitability with respect to $\Omega_{ara}$ decreases from 2010 onward (Figure 4.5b). However, the mean habitat suitability with respect to $\Omega_{ara}$ in the Great Caribbean remains relatively unchanged until 2020, at which point it decreases (Figure 4.5b). In the Red Sea and Persian Gulf, the mean habitat suitability initially increases until 2040, at which point it begins to decrease (Figure 4.5b).
Figure 4.1 Potential reef habitat and habitat suitability in reef locations with respect to SST according to RCP8.5. The light blue shade represents the potential reef habitat defined by the thermal tolerance limits between 21.7°C and 29.6°C. The colour of the charted reef locations indicates the habitat suitability, with red colour means low suitability and blue means high suitability. Reef locations indicated by red dots are reefs where thermal conditions are close to the thermal tolerance limits (i.e. lower or upper tolerance limit), indicate that these areas are already with lower suitability than the reef locations indicated by blue where thermal conditions are close to optima.
Figure 4.2 Potential reef habitat and habitat suitability in reef locations with respect to $\Omega_{asa}$ under RCP8.5. The light blue shade represents the potential reef habitat defined by the lower tolerance limit of $\Omega_{asa}$ beyond 2.82. The colour bar represents the habitat suitability, with red colour means low suitability and blue means high suitability. Reef locations indicated by red dots are close to the lower tolerance limit of $\Omega_{asa}$, indicate that these areas are already with lower suitability than the reef locations indicated by blue dots where conditions are above the lower tolerance limit of $\Omega_{asa}$.
Figure 4.3 Potential reef habitat with respect to SST and $\Omega_{ara}$ under RCP8.5. The light blue shade represents the potential reef habitat defined by thermal tolerance limits between 21.7°C and 29.6°C and the lower tolerance limit of $\Omega_{ara}$ beyond 2.82. The red dots are contemporary coral reef locations.
Figure 4.4 Estimated change in area of potential reef habitat relative to the year 2010 under RCP8.5. Geographic information of six sub-regions is showed in Figure C4.

Figure 4.5 Global and regional mean habitat suitability in reef locations with respect to (a) SST and (b) $\Omega_{\text{ara}}$ under RCP8.5 relative to the year 2010.
4.4 Discussion

4.4.1 Effects of global warming and ocean acidification on potential reef habitats

Global warming and ocean acidification will affect coral reefs by moving the distributions of suitable conditions for coral reefs in the ocean, thus exerting influences on the distribution of potential reef habitat. Rising seawater temperatures due to global warming may lessen low temperature stress in cold waters for corals. With regard to SST, the potential reef habitats showed clearly poleward expansion at high latitudes (Figure 4.1 & Supporting Information Figure C.2). This is consistent with the observed poleward range shift of two common tropical corals, *Acropora sp.*, in the ocean of Japan (Yamano et al. 2011). Likewise, in the southern hemisphere, corals such as *Acropora intermedia, A. microclados, A. monticulosa, A. gemmifera, Goniopora norfolkensis,* and *Plesiastrea versipora* undergo poleward range expansions in both Eastern and Western Australia (Thomson 2010; Baird et al. 2012; Tuckett et al. 2017). The poleward expansion of tropical coral reefs indicate that contemporary reef distributions are limited by a lower thermal threshold and that tropical corals have the potential to colonize suitable habitats when the thermal constraint is removed due to global warming. In contrast, the tropical areas between 20°N and 20°S in the Pacific and Indian Oceans will almost completely lose their potential reef habitats (Figure 4.1) due to temperatures that are beyond the upper thermal threshold for coral reefs (i.e. those above 29.6°C). There is evidence supporting reef retraction with increasing temperature in the tropics in geological records. During the last interglacial period of the Pleistocene (ca. 125000 years ago), coral reefs retracted from the equatorial regions when the global average SST was about 0.5°C higher than today (Kiessling et al. 2012; Hoffman et al. 2017). The expansion of potential reef habitats at high latitudes may not offset the decrease in potential habitats in the tropics, as the area of potential habitats that are lost are much larger than the area of potential habitats gained from warming (Figure 4.1). Globally, the area of potential reef habitats with respect to temperature would still be on a downward trajectory under RCP8.5.

The potential reef habitat with respect to $\Omega_{ara}$ was obtained by setting the lower tolerance limit of $\Omega_{ara}$ to 2.82, which is the lowest observed $\Omega_{ara}$ at global reef locations (Guan et al. 2015). This value should be interpreted as below the level at which reef accretion is restricted; that is, CaCO$_3$ dissolution might exceed CaCO$_3$ production. Retraction of potential reef habitat with respect to $\Omega_{ara}$ starts from high-latitude areas, including the southern GBR, Japan, and the East Pacific upwelling regions (Figure 4.2 & Figure 4.3). This result contrasts with the
findings of Couce et al. (2013), who reported that these areas will be little affected by reducing $\Omega_{\text{ara}}$ (Couce et al. 2013). Couce et al. (2013) argued that SST and light are dominant factors that determine coral reef presence at marginal reef sites (Couce et al. 2013). At present, coral calcification for massive Porites and Diploastrea heliopora at high-latitude reefs is reportedly being affected by warming, which indicates that temperature is likely a dominant factor for high latitude reefs (Cantin et al. 2010; Cooper et al. 2012). However, an increase in coral calcification due to warming does not necessarily ensure coral reef persistence. The persistence of coral reefs depends on the balance of CaCO$_3$ production, physical, chemical, and biological erosion and transport, and CaCO$_3$ dissolution (Kleypas et al. 2001; Eyre et al. 2014, 2018). Many reef corals are capable of buffering their internal pH (McCulloch et al. 2012), and some corals can calcify when $\Omega_{\text{ara}}$ is below 1 (Venn et al. 2013). Although coral calcification decreases with reducing $\Omega_{\text{ara}}$ (Gattuso et al. 1998; Langdon et al. 2000; Marubini et al. 2008), coral calcification only showed a 10–15% reduction per unit change in $\Omega_{\text{ara}}$ (Eyre et al. 2018). However, CaCO$_3$ sediment dissolution is more sensitive to decreasing $\Omega_{\text{ara}}$ than coral calcification, with a 170% change per unit change in $\Omega_{\text{ara}}$ (Trnovsky et al. 2016; Eyre et al. 2018). In addition, unlike biologically mediated coral calcification (McCulloch et al. 2017), CaCO$_3$ sediment dissolution is mostly a geochemical response, which cannot adapt to changing carbonate chemistries (Eyre et al. 2014). Ocean acidification could thus result in net dissolution of coral reefs (Eyre et al. 2014, 2018). Therefore, coral reefs in high latitudes and upwelling regions are sensitive to future reductions in $\Omega_{\text{ara}}$ (Cao and Caldeira 2008; Manzello 2010), since they are currently just finely balanced between calcification, erosion, and dissolution. And the area of potential reef habitats with respect to $\Omega_{\text{ara}}$ would also be on a downward trajectory under RCP8.5 (Figure 4.2).

In this study, a suitable reef habitat is defined as one in which both SST and $\Omega_{\text{ara}}$ are within the tolerance limits. The results clearly indicate that coral reef expansion to higher latitude sites with improved thermal conditions will be limited by decreasing $\Omega_{\text{ara}}$ (Figure 4.3) (Yara et al. 2012; van Hooijdonk et al. 2014). Under the combined influences of SST and $\Omega_{\text{ara}}$, the Great Caribbean region and the Red Sea and Persian Gulf will be affected much later; the whole areas remain as potential reef habitats until 2060-2070 (Figure 4.3 & Figure 4.4). The decline in the area of potential reef habitats in Great Caribbean region, the Red Sea and Persian Gulf are due to $\Omega_{\text{ara}}$ decrease below the lower tolerance limit of 2.82, however, temperature is still within the thermal tolerance limit even with warming (Figure 4.1 & Figure 4.2). By definition of potential reef habitat in this chapter, we do not take into account interactions between temperature and $\Omega_{\text{ara}}$ on coral reefs. Synergistic effect (i.e. when the combined effect is greater
than the sum of individual effects) (Folt et al. 1999) of elevated temperature and acidification were reported on coral calcification and mortality (Anthony et al. 2008; Cooper et al. 2008; Prada et al. 2017). Warming and acidification increase the dissolution of carbonate sediments, however interact antagonistically (Trnovsky et al. 2016). Therefore, the combined effects of warming and acidification on potential reef habitat by considering the net result of CaCO₃ production (coral calcification) and CaCO₃ dissolution are presumably in a declining trajectory (Figure 4.4) and if synergistic effects of warming and acidification into account, the downward slope will be even steeper.

4.4.2 Effects of global warming and ocean acidification on reef habitat suitability

The projected future thermal habitat suitability of contemporary reef locations suggests that corals living in warmer waters, including those of Southeast Asia, the Central Pacific, the Maldives, the Comoro Islands, the Glorieuses, and the Seychelles, will suffer more from warming (Figure 4.1), as tropical coral reefs have been hypothesized to occur very close to their upper thermal limits (Glynn and D’Croz 1990). These areas will become unsuitable due to rising temperature (Figure 4.1), which indicates that these areas would have low potential to support any corals due to their warm conditions.

Southeast Asia and Maldives are hotspots of both coral diversity and fish (Pellissier et al. 2014; Descombes et al. 2015). The absence of reef habitats in hotspots of coral diversity and fish could cause fundamental changes to ecosystem functions and services. In contrast to areas characterized by decreasing thermal habitat suitability, our results showed that high-latitude reefs, including Japan, Hawaii, the northern Red Sea, Persian Gulf, and northern Madagascar and Mauritius, would have an increase in thermal habitat suitability (Figure 4.1), indicating that these areas could serve as temporary refugia from thermal stress. This result is consistent with the findings of other model studies that have found that high-latitude reefs will experience increasing habitat suitability and could serve as temporary refugia (Couce et al. 2013; van Hooidonk et al. 2013, 2014). Warming could result in increased coral calcification in high-latitude reefs (Cooper et al. 2012; Courtney et al. 2017) where the global thermal optima (i.e. 28.7°C) for calcification have not yet been exceeded (Supporting Information Figure C.1).

Our results indicate that thermal habitat suitability in the GBR, the Great Caribbean Region, the Red Sea and Persian Gulf will increase due to warming
(Figure 4.1 & Figure 4.5a). However, the GBR, particularly the northern and central GBR thereof, is threatened by declines in calcification and severe bleaching (Cooper et al. 2008; Hughes et al. 2017, 2018a); this also applies to the Great Caribbean region (Eakin et al. 2010). By using the annual mean SST data, our projections correspond to the expected chronic response of coral reefs to warming rather than acute response such as coral bleaching. Temperature 1°C higher than the long-term highest monthly mean temperature can already cause coral bleaching (Glynn and D’Croz 1990), and when temperature is 2 to 3°C above long-term highest monthly mean temperature for at least 4 weeks can cause severe coral mortality. The annual mean temperature data however smooth out these intra-annual temperature variability that lead to coral bleaching and mortality. Our habitat suitability refers to sustained shifts in environmental condition and we assume that thermal conditions were maintained constant for sufficient time to let the coral acclimate according to their global performance curves.

GBR and Great Caribbean region are experiencing bleaching events in fact, whereas our results predicted these two regions with increasing thermal habitat suitability (Figure 4.1 & Figure 4.5a). Our results suggest that there are factors other than warming that lead to coral bleaching and reduced calcification in these regions. Ocean acidification is reported to lower the coral bleaching threshold (Anthony et al. 2008). Wooldridge (2009) suggested that the loading of dissolved inorganic nitrogen lowers the thermal tolerance of corals in inshore reefs on the GBR (Wooldridge 2009a). De’ath et al. (2012) reported that tropical cyclones are responsible for 48% of coral cover losses in GBR, coral predation by crown-of-thorns starfish (COTS) contributed for 42%, and coral bleaching only accounted for 10% (De’ath et al. 2012). In the Caribbean, the decline in carbonate production has been linked to reduced live coral cover (Perry et al. 2013) due to the decreasing herbivory and increased nutrient input (Aronson and Petch 2001; Mumby 2006). In contrast, the Red Sea is one of the warmest ecosystems on Earth (Chaidez et al. 2017; Krueger et al. 2017), and Red Sea corals are potentially conditioned to extreme SSTs as a result of very high SST variability found in this sea (Ateweberhan and McClanahan 2010). The Red Sea, particularly the Gulf of Aqaba, has been suggested as a reef refugium (Fine et al. 2013) and the coral *Stylophora pistillata* therein has indeed exhibited resistance to warming (Krueger et al. 2017). In summary, on the global scale, our results suggest that the GBR, the Great Caribbean region (with the exceptions of the Cayman Islands and Jamaica), the Red Sea, and the Persian Gulf could serve as potential reef refugia from the stress of warming. These results have strong implications for coral reef conservation and restoration efforts. Habitats such as the GBR and the Great Caribbean should therefore be of high priority when it
comes to protection. Because the main cause of bleaching in these areas may be due to nutrients loading or overfishing, and local protection efforts could mitigate coral reef degradation due to warming.

The areas most affected by reductions in $\Omega_{\text{ara}}$ levels correspond to Southeast Asia, the GBR, the Western Indian Ocean, and the Central Pacific (Figure 4.2 & Figure 4.5b). Caution should be taken when interpreting the increased habitat suitability with respect to $\Omega_{\text{ara}}$ in the Red Sea and Persian Gulf (Figure 4.5b). Coral reef suitability with respect to $\Omega_{\text{ara}}$ decreases when $\Omega_{\text{ara}}$ is higher than the optimum (i.e. 3.82). However, this decrease response with higher $\Omega_{\text{ara}}$ is not supported by the experimental or field studies of coral calcification (e.g. Langdon et al. 2000; Ries et al. 2009; Albright et al. 2016).

We do not know how exactly the combined impacts of SST and $\Omega_{\text{ara}}$ will affect coral reef suitability. However, some conclusions can still be drawn. Increasing thermal habitat suitability (Figure 4.5a) may outweigh the decreasing habitat suitability with respect to reducing $\Omega_{\text{ara}}$ (Figure 4.5b) (Cooper et al. 2012), thus allowing the GBR and the Great Caribbean region to remain potential reef habitats until the years 2050 and 2060, respectively (Figure 4.3). The Red Sea and Persian Gulf remain potential reef habitats and can serve as coral refugia with climate change and ocean acidification due to habitat suitability with respect to SST and $\Omega_{\text{ara}}$ is not declining (Figure 4.5). In contrast, reef habitats in southeast Asia, western Indian Ocean, and Central Pacific will be more impaired due to decreasing habitat suitability with respect to SST and $\Omega_{\text{ara}}$ (Figure 4.5). However, the conditions remaining suitable does not necessarily imply that existing coral community will be able to cope with these changes. Hardy, stress-tolerant, and fast-growing weedy coral species are likely to dominate areas with higher SSTs (Baumann et al. 2016). The slow-growing, long-lived, stress-tolerant coral species are likely to dominate areas with low pH (Fabricius et al. 2011). Thus, the areas such as the GBR, the Great Caribbean, the Red Sea and Persian Gulf could remain potential reef habitats over the coming decades. However, with changing habitat suitability in these areas, the compositions of coral communities may shift to more stress-tolerant species. Note that, our predictions with potential reef habitat and habitat suitability in reef locations are theoretical applications, and we assume that the local disturbances such as eutrophication, pollution, or fishing are removed.
5 Combined effects of multiple environmental factors on coral reefs

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Abstract

Corals depend on a variety of environmental factors such as water temperature, salinity, nitrate, phosphate, and aragonite saturation state. Changes in these conditions can affect coral reef growth and, in the natural environment, many of these variables change simultaneously. The implications of changing conditions on coral growth can be additive, synergistic or antagonistic. In this study we investigate the combined effects of pairwise combinations of five environmental factors on the global occurrence of coral reefs. We use the number of reefs found under the same environmental conditions as a proxy for indicating the suitability of these conditions as a coral reef habitat. Our analysis suggests that the optimal temperature for corals depends on salinity, phosphate, and aragonite saturation state but does not change with nitrate concentration. Optimal salinity and optimal phosphate concentration appear to depend on aragonite saturation state or vice versa. These results suggest that changes in temperature and salinity, temperature and phosphate, temperature and aragonite saturation state, salinity and aragonite saturation state, phosphate and aragonite saturation state will affect corals non-linearly and in a more complex manner than what can be described by an additive model. However, the data suggest that the combined effects of changing nitrate with other factors (i.e. temperature, salinity, phosphate, aragonite saturation state) and salinity with phosphate can be described by adding the responses to individual factors. In addition, our analysis suggests that the response of corals to simultaneous changes in environmental conditions can be both, synergistic or antagonistic, depending on the position in the environmental parameter space relative to the optimal growth conditions.

5.1 Introduction

Coral reefs cover less than 0.2% of the global ocean area (Spalding et al. 2001) but they represent one of the most productive and diverse ecosystems on our planet (Connell 1978; Odum and Odum 1995). Reef-building corals are very sensitive to a number of environmental factors and have relatively narrow tolerance windows (Guan et al. 2015), especially in relation to seawater temperature (Berkelmans and van Oppen 2006; Wooldridge 2009b). Variations of individual environmental factors (e.g. temperature, salinity, or aragonite saturation state) can affect corals’ metabolism (e.g. Muthiga & Szmant, 1987; Ferrier-Pagès et al., 1999) and may have negative consequences for reef survival, such as coral bleaching (Williams & Bunkley-Williams, 1988; Glyn, 1991; Hoegh-Guldberg & Salvat, 1995; Berkelmans & Oliver, 1999; Berkelmans et al., 2004;
Hughes et al., 2017) and reef degradation (Pandolfi et al., 2003; De’ath et al., 2012; Jackson et al., 2014).

Many environmental factors, however, change simultaneously and it is not well understood how coral reefs will respond to these changes in the future. In general, the combined effects of multiple environmental factors can be categorised into three main groups (Folt et al. 1999): (1) additive (when the combined response to changing environmental factors is equal to the sum of individual responses to changing individual factors), (2) synergistic, (when the combined effect is greater than the sum of the individual effects) or (3) antagonistic (when the combined effect is less than the sum of individual effects).

Synergistic effects were reported for the survival of the reef-forming coral Montipora verrucosa when exposed to low salinity (20 psu) and elevated temperature (31°C) in the laboratory (Coles and Jokiel 1978). However, a short-term antagonistic effect on net photosynthesis and photosynthesis to respiration ratio (P:R ratio) was observed when the coral Montastrea annularis was exposed to elevated temperature (33°C) and elevated salinity (40 psu) (Porter et al. 1999). Simultaneous changes in temperature and salinity can, therefore, affect corals synergistically and/or antagonistically depending on the species and conditions. The biomass production, respiration rate, and tissue biomass of the reef-building coral Porites cylindrica in response to nitrate enrichment and elevated temperature and in the absence of particulate food (Nordemar et al. 2003) suggested synergistic effects of nitrate and temperature because corals that were exposed to elevated nitrate appeared to be more stressed by high temperature conditions (Nordemar et al. 2003). Renegar and Riegl (2005), however, reported combined impacts by nitrate and phosphate enrichments on the growth rate of Acropora cervicornis, which could be best described by an additive model at low nutrient concentrations (5 μmol L⁻¹ and 2 μmol L⁻¹ for, respectively, nitrate and phosphate), and by an antagonistic model at high nutrient concentrations (10 μmol L⁻¹ and 4 μmol L⁻¹ for, respectively, nitrate and phosphate). Enhanced mortality of a Mediterranean coral species was attributed to a synergistic effect of ocean warming and acidification (Prada et al. 2017). Additive, synergistic, and antagonistic combined effects of multiple factors are all reported for corals but the reasons for this variety of responses remains unclear.

Non-additive effects may be as common as additive ones (Crain et al. 2008; Darling and Côté 2008). However, the prevalent approach for assessing the combined effects of multiple factors on ecosystems (Halpern et al. 2008; Selkoe et al. 2009) is to apply additive models. This approach is often preferred because of lack of knowledge of where, when or why non-additive combined effects occur.
(Crain et al. 2008; Darling and Côté 2008). The additive model is therefore considered a conservative and feasible option for assessing the combined effects without a clear rationale to include non-additive interactions (Halpern and Fujita 2013). However, the crucial assumption of the additive model is that factors should be independent from one another.

The majority of studies that investigated combined effects of multiple factors were conducted in laboratories on species-level and on short-term, because the conditions for factorial experiments are much easier to control in a laboratory setting (Coles and Jokiel 1978; Porter et al. 1999; Nordemar et al. 2003; Renegar and Riegler 2005; Prada et al. 2017). However, interactions between factors are species-dependent (Bhagooli and Hidaka 2004); and interactions between factors on community and ecosystem level will also depend on ecological interactions, species diversity, trophic complexity, ecological history, and ecosystem type (Vinebrooke et al. 2004). Therefore, extrapolating the combined effects from responses obtained from a single species to a community level may lead to inaccurate, if not erroneous, assessments. Explicit evaluations of the interactions of multiple environmental factors in natural systems remain limited (Darling et al. 2010). Factors may be difficult to manipulate on a community or ecosystem level in the field, and investigating the combined effects of multiple factors on hundreds of coral species is unfeasible.

Here we explore the combined effects of pairwise environmental factors on coral reefs worldwide. We assume that coral reefs have adapted to their environments over evolutionary time scales and that the conditions under which they thrive in the modern ocean can provide relevant information about their physiological adaptations. The number of coral reefs present under specific environmental conditions provides an indication about the optimal conditions under which corals thrive.

5.2 Materials and Methods

In order to investigate if the occurrence of coral reefs worldwide is driven by environmental factors that act independently or in combination, we extracted the environmental conditions (namely temperature (T), salinity (S), nitrate concentration ([NO₃⁻], hereafter N), phosphate concentration ([PO₄^{3-}⁻], hereafter P), and aragonite saturation state (Ω_{ar}) characterising the locations where coral reefs are present and analysed pairwise correlations between environmental factors. We plot the reef occurrences as a two-dimensional
function of all possible combinations of two factors, producing a combined picture of scatter plot and 2D histogram (Figure 5.1).

5.2.1 Coral reef data

Charted reef data were obtained from the Global Distribution of Coral Reefs 2010 (Spalding et al., 2001; IMaRS-USF, Institute for Marine Remote Sensing-University of South Florida, 2005; IMaRS-USF IRD, Institut de Recherche pour le Developpement, 2005) were used to create an ‘observed’ reef habitat distribution, remapped at a 30” × 30” grid cell resolution (Guan et al. 2015).

5.2.2 Environmental data

We considered five physico-chemical environmental variables at sea surface, these were: temperature T (Locarnini et al. 2013), salinity S (Zweng et al., 2013), nitrate N (Garcia et al. 2014), phosphate P (Garcia et al. 2014), and aragonite saturation state Ω. T, S, N, and P were obtained from the World Ocean Atlas (WOA) 2013 in NetCDF format. T and S have a spatial resolution of 0.25° × 0.25°, while N and P have 1° × 1° spatial resolution. Ωara was calculated from Total Alkalinity and Dissolved Inorganic Carbon (DIC) using CO2SYS (Lewis and Wallace 1998). Total Alkalinity and DIC data were obtained from the Global Ocean Data Analysis Project (GLODAP) in NetCDF format (Key et al. 2004). Both datasets have a 1° × 1° spatial resolution. We interpolated the areas that were not covered by the GLODAP dataset (e.g. the Indonesian Sea and the Caribbean). The interpolation algorithm is based on a penalized least squared method (Garcia 2010; Wang et al. 2012). We interpolated DIC and alkalinity, and then used these two interpolated datasets to calculate Ωara.

The resolution of all environmental data was finally adapted to match the spatial resolution of the coral reef data (i.e. 30” × 30”) using the procedure described in the following. Each grid cell of the T and S data was equally divided into 30 × 30 sub-grid cells with values identical to the original grid cell; each grid cell of the N, P, and W was equally divided into 120 × 120 sub-grid cells with values identical to the original grid cell. Therefore, for each grid cell that presented a reef, we could associate the corresponding five physical-chemical variables. For each environmental factor, the tolerance ranges (i.e. minimum and maximum values) within which coral reefs are found at a global scale were obtained from chapter 2. These ranges were: 21.6 – 30.1°C for T, 30.1 – 40.1 psu for S, 0.0 – 10.0 µmol L⁻¹ for N, 0.0 – 0.9 µmol L⁻¹ for P, and 2.82 – 4.3 for Ωara (Guan et al. 2015). For each pair of environmental factors we produced frequency distributions of reefs
based on 2D histograms of number of reefs over 20 equally spaced bins and plotted contour lines.

5.3 Results

We plot the environmental conditions at reef occurrences in relation to pairwise combinations of environmental factors (Figure 5.1, grey dots). The coloured contour lines indicate the cumulation of reefs occurring within determined ranges of environmental conditions. The dashed red lines mark the highest reef occurrence in relation to a single environmental factor (i.e. the optimal condition with respect to the single factor) (more details in chapter 3). The intersection of the two dashed red lines (Figure 5.1A) denotes the hypothetical optimal condition (i.e. the conditions under which the maximum number of coral reefs should be found) if the combined effect of the two individual factors was truly additive.

The contour plot for S and T shows: (1) the distribution is not centred on the intersection of maximum S and T and (2) the optimal temperature for coral reefs varies with salinity and vice versa. For example, at low salinities (e.g. 32-35 psu), the temperature optimum is around 29°C but at high salinities (e.g. 35-37 psu) it reduces to below 28°C (Figure 5.1A and Supplementary Figure D.2). In contrast, the centre of the distribution of reef occurrences is positioned above the dashed line for N, independent of T, S, P, or Ωara (Figure 5.1, panels B, E, H, I and Supporting Information Figure D.2). Moreover, the optimal condition for N (indicated by red contour lines) does not change with T, S, P, or Ωara (Figure 5.1, panels B, E, H, I and Supporting Information Figure D.2). The distribution for P and S is centred close to the intersection of the dashed lines (Figure 5.1F) and the optimum phosphate concentration does not vary much with changing salinity (Figure 5.1F and Supporting Information Figure D.2). The contour plot for T and Ωara (Figure 5.1D) shows a more elaborated pattern although the highest reef occurrence is clearly centred at the intersection of the dashed lines. Multiple peaks can be observed in the contour plots for T-P, S- Ωara, and P- Ωara (Figure 5.1, panels C, G, and J). The 2D histogram for T and P could indicate another relationship where coral reefs are found under higher phosphate concentrations in warmer waters and in lower concentrations in colder water. Coral reefs found at lower salinity or higher phosphate concentrations are also characterised by higher Ωara (Supporting Information Figure D.2).
Figure 5.1 Scatter plots (grey dots) based on pairwise environmental factors at all reef locations; 2-D histograms on top of scatter plots. Red straight lines represent the highest reef occurrence when only a single environmental factor is considered, indicating that the theoretical optimal conditions for each single variable. The optimal condition with respect to each single factor are 28.64 °C for T, 34.8 psu for S, 0.06 mmol L\(^{-1}\) for N, 0.22 mmol L\(^{-1}\) for P, and 3.8 for \(\Omega_{\text{ar}}\). The optimal conditions for coral reefs as a function of pairwise factors (i.e. the combination of environmental factors under which most of coral reefs are found) are indicated by the red contour lines. The intersection of the two straight red lines indicates the theoretical optimal condition if the combined effect of the two individual factors was truly cumulative. However, in case those individual factors affect corals cumulatively, coral reefs would be symmetrically distributed around this optimum.
5.4 Discussion

Coral reefs are not randomly distributed in the ocean because corals have clear dependences on certain environmental conditions where they can survive, grow, and form reefs (Kleypas 1997; Guan et al. 2015). Our results show that these physiological preferences, like the optimal temperature for coral reef growth, may vary in a multidimensional parameter space of environmental conditions and may depend on the environmental variables themselves. However, the underlying assumption of our approach is that the number of reef occurrences can be used as a proxy for illustrating the physiological response of corals to different environmental conditions (chapter 3). In other words, we assume that if more reefs occur under certain environmental conditions, these conditions are more suitable for reef corals and indirectly indicate a better coral physiological performance (e.g. higher calcification rate, higher reef growth rate). This is also the most frequent assumption found in other species distribution models (Guisan and Wilfried 2005).

If the global distribution of coral reefs really reflects the physiological properties of corals, then experimental studies should be designed to account for these physiologically optimal conditions of coral species because the chosen values for the environmental conditions will prescribe the resulting physiological response (e.g. positive or negative and synergistic or antagonistic response). Our results show that the physiological response of corals to changing environmental conditions will depend on the relative position of the environmental conditions in the multidimensional parameter space. If environmental change will affect corals positively or negatively depends on the relative environmental situation with respect to the optimum. Simultaneous changes in temperature and salinity can therefore lead to synergistic affects on coral growth at low salinities (Coles and Jokiel 1978) and to antagonistic effects at high salinities with warming (Porter et al. 1999). These physiological responses are pictured in the 2D histogram for S and T that the temperature optimum is higher at lower salinity and lower at higher salinity (Figure 5.1A).

In the simplest situation of two factors A and B interacting additively, the response to changes in factor A is independent of responses to changes in factor B (Dunne 2010). In this case we could infer that the optimal condition of factor A is independent of factor B. We find that the combined effects of nitrate and other factors are additive (Figure 5.1 & Supporting Information Figure D.2), which lends support for studies that applied an additive model (Halpern et al. 2007, 2008; Selkoe et al. 2009). Changes in nitrate concentrations do not interact with the pH influence on corals (Marubini and Atkinson 1999). However, in a
synergistic relationship with ocean warming, DIN loading can decrease the bleaching threshold (Wooldridge 2009a; Wooldridge and Done 2016). Thermal bleaching triggered by high temperature within short time is an acute response of corals, which is not included in our results. Our results rather reflect the chronic, long-term changes of combined impacts of nitrate and warming within the tolerance limits of coral reefs. Elevated nutrients may contribute to the spread of coral diseases (Bruno et al. 2003; Voss and Richardson 2006) and also contribute indirectly to coral reef decline by increasing the productivity of macroalgae (McCook et al. 2001). Temperature, salinity, and $\Omega$ on the other hand affect reef corals directly. The additive model may be appropriate when factors affect different physiological or ecological processes (Folt et al. 1999). Hence, nitrate additively interacting with other factors seems to be a reasonable assumption.

Our results show, however, that (1) the distribution of optimal conditions (indicated by higher reef occurrences) of T depends on S, P, and $\Omega_{ara}$; (2) the distribution of optimal conditions of S depends on P and $\Omega_{ara}$, and (3) the distribution of optimal conditions of P depends on $\Omega_{ara}$ (Figure 5.1 and Supporting Information Figure D.2). We therefore suggest that T and S, T and P, T and $\Omega_{ara}$, S and $\Omega_{ara}$, P and $\Omega_{ara}$ are not independent and interact non-additively on the performance of corals. The distribution, however, of optimal conditions (indicated by higher reef occurrences) of T depends on S, P, and $\Omega_{ara}$; and the distribution of optimal conditions of S depends on P and $\Omega_{ara}$; the distribution of optimal conditions of P depends on $\Omega_{ara}$ (Figure 5.1 & Supporting Information Figure D.2). We therefore suggest that T and S, T and P, T and $\Omega_{ara}$, S and $\Omega_{ara}$, P and $\Omega_{ara}$ interact non-additively on the physiological performance of coral reefs. Furthermore, $\Omega_{ara}$ is calculated with CO2SYS software (Python version) as a function of temperature, salinity, phosphate and other factors (i.e. alkalinity, pCO$_2$, and silicate). The complicated relationship we found from the 2D histogram of T - $\Omega_{ara}$, S - $\Omega_{ara}$, and P - $\Omega_{ara}$ may indicate causal interactions. Thus, the impacts of $\Omega_{ara}$ cannot be separated from T, S or other factors. However, our tests in the present study are not sufficient to detect the complicated relationships between these factors and more tests should be applied in the future under controlled laboratory or field conditions.

The relative effects of environmental factors and their combinations may be species specific and, therefore, depend on species assemblage (Vinebrooke et al. 2004) and magnitudes of environmental factor change. Environmental factors may be difficult to manipulate in the field in order to investigate the combined impacts on a community or on ecosystems locally or globally. However, our global assessment may provide insights on the combined effects of pairwise
environmental factors can have on coral reefs and may provide valuable hints for further laboratory experiments. Our study is thus a first step in the investigation of the combined impacts on coral reefs on a global basis. A next step would be to quantify the pairwise or even higher dimensional relationships between environmental factors and physiological responses under controlled conditions in the laboratory or in the field.
6 General discussions

6.1 The geologic history of coral reefs

The long-term survival of coral reefs depends on how well they can deal with environmental change. Variations in sea surface temperature, seawater chemistry, sea level and global concentration of atmospheric CO$_2$ have occurred over the last 540 million years (Phanerozoic Eon) (Pandolfi and Greenstein 2007; Pandolfi and Kiessling 2014). The fossil records offer the chance of investigating the long-term pattern of climate change (e.g. magnitude change of temperature and CO$_2$) and coral reef response to these changes.

![Diagram](image)

**Figure 6.1** Sampled diversity of reef building corals in the Phanerozoic. Sampled diversity counts the number of occurrences of the selected taxa in each Age bin within the selected geographic extent. Rectangular boxes and arrows mark major events occurred on coral reefs and their potential causes and consequences. Data for generic diversity are from Paleobiology Database. The data were downloaded from [https://paleobiodb.org/navigator/](https://paleobiodb.org/navigator/) on 15 Oct, 2018. Order: Tabulata, Rugosa, Scleractinia. Region: -180.0° to 180.0° N, -90.0° to 90.0° E.

Over geologic time, the inorganically precipitated calcium carbonate varied between calcite dominant and aragonite dominant due to shifts in the magnesium/calcium (Mg/Ca) ratio (Ridgwell and Zeebe 2005). CO$_2$ level was 25
times higher than that of today during the early Palaeozoic, followed by a drop to 306 ppmv near the end of the Devonian (Pandolfi and Greenstein 2007). Early to mid-Palaeozoic reef ecosystems were in the calcite dominant phase (Ridgwell and Zeebe 2005), and calcareous stromatolites, calcareous Cyanobacteria, archaeocyaths, algae, sponge, and corals were the principal reef-building organisms (Newell 1972; Kaźmierczak et al. 1985; Rowland and Gangloff 1988; Riding 1991). The corals of this period were non-scleractinian tabulate and rugose corals (Newell 1972). A brief glacial interval caused the Late Ordovician extinction (443.8 Mya) (Sheehan 2001), resulting in 22% of marine taxonomic losses. However, reef communities including rugose and tabulate corals and stromatoporoid sponges recovered rapidly, and they were the important community in the Silurian reef (Droser et al. 2000; Krug and Patzkowsky 2004). Cooling of low-latitude surface water by 5-7°C, oceanic anoxia, and sea-level change have been suggested to have caused of the Late Devonian mass extinction (ca. 374 Mya) (Joachimski and Buggisch 2002; Bond and Wignall 2008; De Vleeschouwer et al. 2017), which resulted in a 21% decline in marine species diversity and reef collapse (Droser et al. 2000). Major Devonian reef builders including tabulate corals and stromatoporoid sponges experienced decline in diversity and did not recover for the remainder of the Paleozoic (Figure 6.1) (Copper 1994; Droser et al. 2000). After the Late Devonian mass extinction, seawater chemistry shifted from low Mg/Ca ratio to higher Mg/Ca ratio, thus aragonite became the dominant chemical phase (Ridgwell and Zeebe 2005). A rapid temperature rise of 15°C over the Permian-Triassic boundary (ca. 0.8 Mya), acid rain, ozone depletion, and oceanic anoxia caused the End Permian mass extinction (ca. 251 Mya) (Wignall and Twitchett 1996; Sun et al. 2012; Black et al. 2014), where up to 96% of marine species and 70% of terrestrial species were lost (White 2002). All Paleozoic corals, tabulate coral and rugose corals, died out during this event (Figure 6.1) (Stanley 2003).

Reef recovery took 8 myr (in Middle Triassic) after the end-Permian crisis (Kiessling et al. 2002; Stanley 2003; Pandolfi and Kiessling 2014). Since Middle Triassic (241 Mya), scleractinian corals appeared and became increasingly dominant reef-builders (Stanley 2003). The end-Triassic (201 Myr) extinction and reef collapse was linked to warming of 8-10°C over 0.6 myr and a rapid release of CO₂ as a result of flood basalt volcanism, which led to a temporary undersaturation of sea water with respect to aragonite and calcite (Hautmann 2004; van de Schootbrugge et al. 2007; Korte et al. 2009; Schoene et al. 2010; Whiteside et al. 2010), causing a substantial extinction among marine species, including scleractinian corals and sponges. However, 12 families of corals survived while 3 went extinct (Hallam 2002). Recovery from the end-Triassic took about 0.5 Myr after the extinction (Kiessling et al. 2009; Lathuilière and
Marchal 2009; Pandolfi and Kiessling 2014). Elevated pCO₂, global warming and increased surface water stratification inducing anoxic conditions led to the Toarcian Oceanic Anoxic Event (ca. 183 myr) (Harries and Little 1999; Izumi et al. 2012) and resulted in a major reef crises although extinctions were modest (Pandolfi and Kiessling 2014).

In the Cretaceous period (145-66 Mya), reefs were dominated by rudists after the Cenomanian-Turonian anoxic event (ca. 92 mya) (Jenkyns 1980; Pandolfi and Kiessling 2014). However, coral diversity remained high although corals seem to have lost their reef building potential (Stanley 2003; Pandolfi and Kiessling 2014). Rudists takeover has been attributed to the low Mg/Ca ratio of seawater (Stanley and Hardie 1999; Ries 2010) and warm water conditions (Johnson 2002; Pandolfi and Kiessling 2014). The rudists died out in the terminal Cretaceous mass extinction (Stanley 2008).

The Paleocene-Eocene Thermal Maximum (PETM) at 56 million years ago was attributed to a volcanism associated rapid rise of carbon into the atmosphere (Guţăhr et al. 2017), leading to 4 - 5°C warming during 20 thousand years (Jones et al. 2013). Tropical sea surface temperatures may have exceeded 40°C (Aze et al. 2012), reef corals were replaced by larger benthic foraminifera (Speijer et al. 2012) and reef production declined dramatically (Scheibner and Speijer 2008). The PETM was however mainly accompanied by a massive release of methane and CO₂ was secondary source (Gehler et al. 2016). From the middle to late Eocene, typical reefs dominated by coral assemblages became the most common type of bio-construction and corals had established diversity comparable to today (Scheibner and Speijer 2008).

Within the Quaternary Period, there were periodic variations of CO₂, temperature, and sea level (Pandolfi and Greenstein 2007). At the onset of each warm interval, CO₂ increased by 8 to 10 ppmv per thousand years, and temperature increases of between 0.5 to 1.0°C per thousand years (Petit et al. 1999; Pandolfi and Greenstein 2007). Coral species and coral reefs underwent dramatic changes in abundance and distribution during Quaternary (Pandolfi and Greenstein 2007). For example, during the last interglacial period of the Pleistocene (ca. 125,000 years ago), corals retracted from the equatorial regions when the average SST was at least 0.5°C warmer than today (Kiessling et al. 2012; Hoffman et al. 2017), and migrated to higher latitude where suitable condition were present in response to climate change (Pandolfi and Kiessling 2014).
In summary, during the Phanerozoic (past 540 Mya), temperature was up to 6°C higher than today in the tropics, and CO₂ was up to 20 times higher (> 6000 ppmv) (Ridgwell 2005; Pandolfi and Greenstein 2007). Compared to the long-term pattern (> 10⁴ to 10⁵ years), the magnitude of predicted climate change is within the past long-term history (Pandolfi and Greenstein 2007). Compared to more recent pattern in temperature during the Quaternary, the predicted magnitude and rate of warming for the next century (1.2 to 5.8°C/century) are also within climate change during the Quaternary (Pandolfi and Greenstein 2007). However, the predicted magnitudes and rates of CO₂ (111 to 732 ppmv/century) far exceed the Quaternary (3.4 ppmv/century) (Pandolfi and Greenstein 2007). Coral reefs, however, existed throughout the Phanerozoic. Coral reefs experienced various global mass extinction events and reef collapse (e.g. end Permian, end Triassic, PETM) corresponding to global perturbations. However, coral reefs reappeared after such events, possibly because some corals outpaced the unfavourable conditions, like the 12 families that survived the end-Triassic extinction (Hallam 2002), or because some corals were in refugia, such as those in the Limalok Guyot during the PETM, which remained unaffected. (Robinson 2011).

6.2 Using the past to predict the future

6.2.1 Response of coral reefs to warming

In the past, coral reefs have migrated in response to warming. There have been major periods of worldwide reef expansion, for example in the mid-Silurian-Late Devonian, the Late Pleistocene, and the Last Interglacial, corresponding to average temperatures above those of the present (Copp 1994; Precht and Aronson 2004; Kielssing et al. 2012). In recent years, the poleward expansion of reef corals has already been observed in the waters of Japan and Australia (Thomson 2010; Yamano et al. 2011; Baird et al. 2012; Tuckett et al. 2017). This poleward expansion is attributed to a warming ocean, which has occurred at a rate of approximately 0.35°C over the last 50 years (Baird et al. 2012). The results reported in chapter 4 concerning temperature are in agreement with previous findings that warming causes a poleward coral reef expansion in higher latitudes (Figure 4.1). In contrast, reef corals retracted (i.e. decline in diversity) due to warming during the last interglacial, with an average SST of 0.5°C higher than that of the present (Kielssing et al. 2012; Hoffman et al. 2017). Our results (chapter 4) also indicate that habitat suitability in tropical regions will be negatively affected by warming (Figure 4.1). However, increased reef expansion may be offset by losses in the equatorial regions (Figure 4.2).
6.2.2 Response of coral reefs to marine chemistry

The influence of seawater chemistry on skeletal mineralogy appears to be particularly significant for reef-building corals. The Mg/Ca ratio and saturation state of carbonate in seawater exert a profound influence on the mineralogy of coral skeletons and the success of reef-building coral reefs. For example, one solitary non-reef building scleractinian coral in the Late Cretaceous (when the Mg/Ca ratio was approximately to 1) has been reported as having had a calcite skeleton (Stanley 2008). An experimental study has demonstrated that modern scleractinian corals precipitate more calcite skeletons when the Mg/Ca ratio in seawater is lowered (Ries et al. 2006). A low Mg/Ca ratio can reduce the coral calcification rate (Ries et al. 2006), whereas a lower Mg/Ca ratio favours rudists’ dominantly calcitic mineralogy and rudist takeover occurred on reefs during the Late Cretaceous (Stanley 2008; Pandolfi and Kiessling 2014). The flourishing of reef-building corals over the past 30 million years coincided with a rise in the Mg/Ca ratio and a reduction in atmospheric CO₂ (Stanley 2008).

Corals have experienced very high levels of atmospheric CO₂ over geological time. For example, the CO₂ level during the Late Cretaceous has been estimated at approximately twice the modern-day level (Ridgwell 2005). Past high CO₂ levels resulted in sea surface pH and CO₃²⁻ concentrations that were lower than those of the modern ocean (Tyrrell and Zeebe 2004; Ridgwell 2005). Given that they were able to survive under these conditions, it seems that corals can develop different physiologies under acidified conditions. Experiments have found that corals have the capacity to buffer their internal pH and DIC against changes in the external environment (Wall et al. 2015; McCulloch et al. 2017). Fine and Tchernov (2007) have demonstrated that corals grown in experimental acidified conditions (pH: 7.3) can live without skeleton (Fine and Tchernov 2007). Note that oceanic Ca²⁺ concentrations in the past have been estimated as being much higher than those found in the modern ocean (e.g. during the Late Cretaceous, the Ca²⁺ level was 23 mmol kg⁻¹; while in the modern ocean, the Ca²⁺ level is 10 mmol kg⁻¹) (Tyrrell and Zeebe 2004; Pandolfi and Greenstein 2007), with the result that the surface ocean saturation state with respect to calcite and aragonite in the past was nearly the same as that of the modern ocean (Stanley 2008; Ridgwell and Schmidt 2010).

A critical factor is that, at present, the Ca²⁺ concentration in the ocean happens to be at its lowest level for the last 100 million years (Tyrrell and Zeebe 2004). This circumstance makes the anticipated rise of atmospheric CO₂ especially
problematic because the reduction in CO$_3^{2-}$ concentration, in combination with a relatively low Ca$^{2+}$ concentration in seawater, is likely to produce an exceptionally low saturation state for seawater with respect to calcium carbonate. Under scenario RCP8.5 (chapter 4), the predicted aragonite saturation state in contemporary reefs is expected to decrease below the lower tolerance of coral reefs by the year 2100 (Supporting Information Figure C.3), resulting in the absence of potential reef habitats with respect to $\Omega_{\text{ara}}$ (Figure 4.2). During the range expansion of coral reefs due to warming (e.g. during the mid-Silurian-Late Devonian, the Late Pleistocene, and the Last Interglacial), there were no rapid rises in CO$_2$, so corals could migrate into cooler waters where chemical conditions were favourable. However, in the contemporary world, ocean acidification is likely to limit the poleward expansion of corals into higher latitudes (Figure 4.3, chapter 4) (Yara et al. 2012).

### 6.2.3 Coral reef adaptation

It is important to determine whether coral reefs have the ability to adapt to global warming and ocean acidification. Corals have demonstrated a capacity to rapidly adapt to warming via symbiont shuffling or switching. Reef corals live in close association with *Symbiodinium* and a range of bacteria, fungi and viruses (Torda et al. 2017; Webster and Reusch 2017); variation in these symbionts can contribute to coral acclimation. *Symbiodinium* have distinct physiological optima; for example, clade D is more resistant to thermal stress than clade C (Stat and Gates 2011). Corals that increase the relative abundance of *Symbiodinium* clade D can increase their thermal tolerance by 1 – 1.5°C (Berkelmans and van Oppen 2006; Jones et al. 2008; Oliver and Palumbi 2011a, 2011b). Changes in the composition of bacterial communities can result in shifts in corals' metabolic activities and may provide scope for corals to acclimate to warmer temperatures (Torda et al. 2017; Ziegler et al. 2017; Grottoli et al. 2018). Another mechanism by which corals can adapt to warming is through physiological acclimatisation of the coral host or the *Symbiodinium* zooxanthellae. Studies have found that corals can acclimate to warming and ocean acidification by increasing their expression of heat-shock protein and controlling their gene expression (Barshis et al. 2013; Palumbi et al. 2014; Bay and Palumbi 2015; Moya et al. 2015; Putnam et al. 2016; Torda et al. 2017). Finally, the composition of coral communities can also shift towards tolerant species in response to warming. Warming results in changes to a coral community towards hardy, stress-tolerant, and fast-growing weedy coral species (Baumann et al. 2016). However, ocean acidification could shift coral communities towards slow-growing, long-lived, stress-tolerant coral species (Fabricius et al. 2011). From the Neogene (22 Mya) to the present, long-term
changes in climatic and oceanic circulation patterns across the Caribbean have presumably resulted in the local reef coral fauna taking the form of large, long-lived colonies (Johnson et al. 1995). Reef corals thus have various biologically mediated strategies with which to adapt to warming and ocean acidification, whereas the dissolution of reefs is primarily a geochemical response to changes in seawater chemistry (Eyre et al. 2014).

The results presented in chapter 4 suggest that, on the global scale, there are reef habitats that will still remain potentially habitable over the coming decades, such as those in the GBR, the Great Caribbean, the Red Sea, and the Persian Gulf (Figure 4.3). However, given the changing habitat suitability of these areas due to warming and ocean acidification, the compositions of coral communities may shift to favour more stress-tolerant species. Hoegh-Guldberg (2007) has suggested that climate change is likely to hinder migration and the successful proliferation of alleles from tolerant populations (Hoegh-Guldberg et al. 2007). Under these conditions, areas such as the GBR are likely to shift from coral-dominated reefs to eroding rubble banks over the next 50 to 100 years (Hoegh-Guldberg et al. 2007). It seems unlikely that adaptation will solve the problems faced by coral reefs as a result of global climate change. Geological evidence indicates that calcifying marine organisms, including corals, indeed suffered periods of reductions in diversity and reef collapses as a result of significant and rapid changes in CO2 and the associated warming and ocean acidification (e.g. the End Permian, the end-Triassic, and the PETM). However, it has also been suggested that adaption will not be rapid enough to keep pace with future ocean warming under RCP8.5 scenario (Bay et al. 2017).

6.2.4 Major challenge for contemporary coral reef

There are two major differences between the challenges that reefs were confronted with in the past and those that will arise in the coming decades. The first is that the changes in the rate and magnitude of CO2 increase that are taking place in the present world appear to be unprecedented in the history of our planet (Pandolfi and Greenstein 2007). The second difference is that today’s reefs are also severely affected by anthropogenic disturbances such as overfishing and pollution (Hallock and Schlager 1986; Hughes 1994; Hughes et al. 2003; Pandolfi et al. 2003). Anthropogenic pollution results in excess nutrient input, which stimulates the growth of plankton, which in turn reduces water transparency, and macroalgae, which compete with corals for space and light. In Jamaica, corals have declined by approximately 45% from 1970 and reefs have experienced a dramatic phase shift from coral-dominated to macroalgae-
dominated due to human and natural disturbances (Hughes 1994). The results presented in chapter 3 suggest that 26% of coral reefs will experience decreased habitat suitability due to elevated nitrate and/or phosphate concentrations. These locations are additionally found in the central and southern GBR, along the Persian Gulf, the coasts of Oman, Kenya, Tanzania, and near the islands of the Central Pacific (along 20°S). Furthermore, more than half of the global coral reefs face both local and global threats (i.e. warming and ocean acidification), especially in Southeast Asia, the Great Caribbean, the Western Indian Ocean, and in the Central Pacific (see chapter 3 for details). Thus, in the absence of immediate attempts to protect coral reefs, elevated nutrients and overfishing are likely to impede the ability of coral reefs to survive, even though temperature conditions may theoretically be suitable.

6.3 Future predictions

6.3.1 Species distribution models

Species distribution models (SDMs) are the main tools used for understanding species distributions in the past, present, and future and for understanding the factors that limit the species. Commonly used species distribution models are, for example, Generalized Linear Models (GLM), Maximum Entropy Models (Maxent), Generalized Additive Models (GAM), and classification and regression trees (CART). In addition, generalized Linear Models (GLM) and Maximum Entropy Models (Maxent) are commonly used to predicting coral reef distributions (e.g. Freeman 2015; Freeman et al. 2013; Couce et al. 2013; Couce et al. 2012; Descombes et al. 2015). The ReefHab model (Kleypas 1997) is an alternative option to species distribution models. By setting the tolerance limits of coral reefs, ReefHab predicts if a reef is present or absent at a specific location. In chapter 2, ReefHab is first applied in an inverse way to find the minimum and maximum values of environmental variables at reef locations, and the minimum and maximum values are used as tolerance limits for potential reef habitats. By updating the coral reef tolerance limits, the predicted potential reef habitats are with higher accuracy compared to the results with the old tolerance limits from Kleypas (1997). Besides the results of presence or absence of potential reef habitat (chapter 3), by fitting the frequency distribution of coral reefs along the variable gradient, a parametric function of habitat suitability with respect to each environmental variable within potential reef habitat is calculated.

In generalized Linear Model (GLM), the expected value of dependent variable Y is transformed by a link function and the transformed variable Y is linearly linked
to the independent variables (Guisan et al. 2002). The distribution of the dependent variable Y in GLM is generated from an exponential family including Gaussian, exponential, binomial, Poisson, or gamma distributions, and the link function can be any monotonic differentiable function including logarithm or logit (Guisan et al. 2002). Thus, for GLM, the shape of the dependent variable Y can be described by a parametric function. The Generalized additive model (GAM), however, represents a non-parametric regression type (Hastie and Tibishirani 1986). The Generalized additive model uses a section of the data at each time, and fit each section by smoothing spline or polynomial regression, and then join the separated fitting sections together (Hastie and Tibishirani 1986). The Classification and regression tree (CART) is constructed by repeatedly splitting the response variable into two mutually exclusive groups along the explanatory variable and develop a classification decision tree (De'ath and Fabricius 2000). Each group is as homogeneous as possible with regards to the response variable. Maximum Entropy Model (Maxent) assumes that environmental variables act as constrains on the distribution of a species, the approximation of the probability distribution of dependent variable Y satisfies any constraint, and that within those constraints, the species distribution should have maximum-entropy (i.e. that is being most spread out, or the probability distributions are as similar as possible to a uniform distribution) at known occurrence sites (Phillips et al. 2004, 2006; Phillips and Dudík 2008). Maxent does not develop a parametric function of the dependent variable Y. ReefHab does not develop a parametric function either. In chapter 2, ReefHab finds locations with environmental conditions that satisfy the tolerance limit considered into the model (Kleypas 1995, 1997). In chapter 3, parametric function of habitat suitability is calculated by fitting the frequency distribution of coral reefs along the variable gradient.

When applying GLM, GAM, and CART to predict the probability of presence of a species, both presence and absence data are needed. GAM can also predict with presence-only data, however, GAM performs better when the absence data is added (Zaniewski et al. 2002). In contrast, Maxent is based on presence-only data, which can avoid the problems of unreliable absence records (Phillips et al. 2006; Phillips and Dudík 2008; Elith et al. 2011). ReefHab and the method applied in chapters 2 and 3 use both presence and absence data. Comparing predictions of coral reef potential habitats, ReefHab can generate predictions with higher accuracy (Guan et al. 2015) than Maxent (Couce et al. 2012). However, when only sampled species distribution data exist (i.e. presence-only), Maxent is a robust tool for predicting potential habitat for corals (Davies et al. 2008; Tittensor et al. 2009; Davies and Guinotte 2011; Yesson et al. 2012).
Environmental variables from sampled locations may be biased due to sample efforts and may not reflect the whole tolerance range of corals.

SDMs are calibrated within a set of particular conditions defined by the training data (or sample data). When making predictions based on future environmental conditions, the new conditions are typically different than the range of conditions used to calibrate the model (Loehle and LeBlanc 1996). Thus SDMs may produce unrealistic results (see Supporting Information of Couce et al. 2013).

![Figure 6.2](image)

**Figure 6.2** Suitability response curves for environmental variable considered when projecting for future novel condition. Three examples of extrapolation methods: linear extrapolation (a), by assuming constant values (b), or following the equation used in the regression model (c). Modified from Merow et al. (2013) and Couce et al. (2013).

For GLM, the shape of suitability response curve, especially for the extrapolation area, can be described by a parametric function (e.g. Figure 6.2c). The primary way Maxent treats extrapolation to novel conditions is “clamping”: that is assuming that the response is held constant outside the range of model calibration (Figure 6.2b). The method “clamping” of extrapolation in Maxent makes the predictions less reliable, because “clamping” is unlikely to reflect biological reality (Merow et al. 2013). For example, it is already shown that extreme environmental condition such as temperature or pH is lethal, yet the “clamping” in Maxent constantly holds the same response as they were at the limit condition. The linear extrapolation (Figure 6.2a) is also tested in Couce et
al. (2013). However, the resulting prediction yields an increasing suitability with temperature higher than 30°C for coral reefs, which goes against known physiological responses of coral reef ecosystems. Appropriate extrapolation methods should be chosen based on the physiological response of the organisms and caution should be taken when interpreting the projections derived from Maxent. With no parametric function and no restriction on the data, GAMs will lose predictability by yielding spurious values when extrapolating to new conditions (Thuiller et al. 2004). CART partitions data along the explanatory variable, and each interior node is determined by the training data, and will be identical when new data is added. Thus, when new data that is out of the range is added to CART, it will always fall into a subset that is partitioned with training data. The habitat suitability functions used in chapters 3 and 5 are constructed by using the global coral reef presence data in order to get whole tolerance range of coral reefs to environmental variables and the skew normal shape of the habitat suitability functions are supported by physiological studies (Pörtner 2002; Pörtner and Knust 2007; D’Angelo and Wiedenmann 2014). By applying the suitability functions in chapters 3 and 5, the extrapolation difficulties can be overcome.

6.3.2 Identifying current reefs

Due to the impacts of salinity, nutrients, sedimentation, and light penetration, the environmental conditions at large tropical river mouths and within the Bay of Cartagena (Restrepo et al. 2006) are not considered as suitable habitat for coral reefs. However, a coral reef system of 9500 km², spanning from 5°N to 1°S and 44° to 51°W, was recorded between the Brazil-French Guiana border (Moura et al. 2016) (Figure 6.3a). In addition, Orbicella spp. dominated coral reef are found in Cartagena Bay (10°18’10”N, 75°34’55”W) (López-Victoria et al. 2015) (Figure 6.3a). These two newly identified coral reefs in turbid and eutrophied waters are contrary to expectations. These two new coral reefs are not recorded in the observed coral reef dataset (Figure 6.3b), although these two areas are predicted as potential coral reef habitats by ReefHab with updated tolerance limits in chapter 2 (Figure 6.3a). The ReefHab using the updated tolerance limits thus can be used to identify new coral reefs. The potential reef habitats are of interest for reef conservation and restoration, as they are located in areas that are potentially habitable, and may be used to plan reintroductions of species or relocate reserves.
Figure 6.3 Figure (a) Potential reef habitats predicted by ReefHab (blue) and newly discovered coral reefs (red) (b) Observed coral reefs (blue). The geographic information of newly discovered coral reefs is extracted manually from Fig. 1 in Moura et al. (2016) and from Fig. 1 in López-Victoria (2015).

6.4 Data limitations

In chapter 4, ensembles of climate models for future projections of monthly mean sea surface temperature (SST) and $\Omega_{\text{ara}}$ under emission scenario RCP8.5 are taken from van Hooidonk et al. (2014) (downloaded from http://onesharedocean.org/public_store/oo_aragonite/download.html). Van Hooidonk et al. (2014) obtained SST, surface pressure of CO$_2$, pH, and salinity from fully coupled models in the Coupled Model Intercomparison Project 5 (CMIP5; http://pcmdi9.llnl.gov/esgf-web-fe/) (van Hooidonk et al. 2014). Thirty three available models that predicted SST were used, and model mean temperatures were adjusted based on the OISST V2 1982-2005 climatology (van Hooidonk et al. 2013, 2014). SST, surface pressure of CO$_2$, pH, and salinity were used to calculate $\Omega_{\text{ara}}$ (van Hooidonk et al. 2014). Nine available models that archived all four variables are used for calculating $\Omega_{\text{ara}}$ (van Hooidonk et al. 2014).
Figure 6.4 Variation of annual mean between the ensemble projecting SST and $\Omega_{\text{ara}}$ (van Hooidonk et al. 2014) and observation (WOA2013) in 2013. Red represents an overestimation of the model data compared to observations, while blue represents an underestimation of the model data compared to observations.

The ensemble projection of SST and $\Omega_{\text{ara}}$ data are probably the best data available. However, the projection data still have variations compared to observations (Figure 6.4). For example, the ensemble model data of SST is overestimated in Southeast Asia compared to observations, whereas the ensemble model data of $\Omega_{\text{ara}}$ is underestimated. This could result in lower habitat suitability with respect to both SST and $\Omega_{\text{ara}}$ in Southeast Asia (chapter 4). Thus, care should be taken when interpreting the results presented in chapter 4.

6.5 Future perspectives

Species distribution models such as ReefHab implicitly assume that species occur in all environments where it is possible for them to survive and that these potential habitats are entirely defined by environmental conditions including temperature, salinity, pH, etc. However, the geographic range of a species is also influenced by dispersal, competition with other species, or habitat type (e.g. rock, mud, or sand). One of the most common ways for coral reproduction is broadcast spawning. Coral larvae are mainly transported by the ocean currents for days to months (Kendall et al. 2013). Depending on seafloor conditions, the larvae may
attach to the substrate and grow into a new coral colony. Moreover, larval dispersal is also determined by biological factors (e.g. duration of larval competency, mortality, and vertical position of larvae in the water column) (Nozawa and Okubo 2011). Larval life-stage duration depend on temperature, more specifically, the duration time decrease with rising temperature (Gillooly et al. 2002; O’Connor et al. 2007). Warming potentially decreases the length of time that larvae are transported by the currents and are exposed to predators. In addition, ocean acidification has negative impacts on larval settlement and polyp growth (Albright et al. 2008; Suwa et al. 2010; Nakamura et al. 2011). Coral larvae are exposed to environmental factors simultaneously and the combined impacts of environmental factors are not easy to disentangle. Ocean currents can rapidly disperse larvae into new habitats, but the capacity to deliver individuals, biological impacts on larvae, and interactions between environmental factors have not been considered in this thesis. Further research efforts should focus on better understanding the coral reef biogeography under climate change.
Key findings and significance

While covering approximately 0.1% of the world’s ocean surface, coral reefs are among the most productive ecosystems on Earth, create habitats for 25% of all marine species, and provide valuable ecosystem services to humans (Spalding and Grenfell 1997; Moberg and Folke 1999). Coral reef habitats are typically characterised by waters with temperature and salinity above, respectively, 18°C and 32 psu. High temperature, however, causes coral bleaching and coral mortality. High nutrient concentration creates unsuitable conditions for corals by stimulating the increase of algae, direct coral competitors for light and space. At the same time, ocean acidification impairs coral calcification and accelerates CaCO₃ dissolution; making reef formation more difficult. Ocean warming, ocean acidification, eutrophication, and other environmental perturbations can therefore have negative consequences on coral reefs by reducing the current habitat suitability and their potential habitat. In this context, tolerance limits of coral reefs and how coral reefs will respond to environmental perturbations are fundamental aspects to consider if we are to understand coral reef distributions on global scales. With reference to the six key objectives, the major findings of this thesis are:

1. The global, annually averaged tolerance limits for coral reefs are 21.7-29.6°C for SST, 28.7-40.4 psu for salinity, 4.51 μmol L⁻¹ for nitrate, 0.63 μmol L⁻¹ for phosphate, and 2.82 for Ωara. The averaged minimum light intensity in coral reefs is 450 μmol photons m⁻² s⁻¹ (chapter 2).

2. Within the tolerance limits, coral reefs respond to environmental changes nonlinearly with global optima at 28.7°C, 3.8, 0.15 μmol L⁻¹, 0.16 μmol L⁻¹ for SST, Ωara, nitrate, and phosphate respectively (chapter 3).

3. When taking into account regional or species-specific adaptations, about 17% of reef locations in the six major coral reef regions will be under global threats of warming by 0.1°C and/or a decline in Ωara by 0.02. About one fourth of the reefs will be under local threats, if nitrate and/or phosphate will increase by 0.02 μmol L⁻¹ and 0.01 μmol L⁻¹, respectively. While only 3% of reef locations will constitute temporary refugia (i.e. habitat suitability improved by temperature, Ωara, nitrate, and phosphate) including the Nansha Islands (the Spratly Islands), the Andaman and Nicobar Islands, the Northern Red Sea, and the Turks and Caicos Islands, more than half of reef locations will be affected by both global and local threats under changing environmental conditions (chapter 3).

4. The tolerance limits for SST and Ωara are used for predicting potential reef habitat under CO₂ emission scenario RCP8.5 (chapter 4). The poleward extension of coral reefs due to warming will be limited by acidification.
5. Warming will improve habitat suitability at the Great Barrier Reef (GBR), the Great Caribbean region (except Cayman Islands and Jamaica), and in waters of Japan, Hawaii, northern Red Sea and Persian Gulf. In contrast, habitat suitability in Southeast Asia, Central Pacific, Maldives, Comoro Islands, Glorieuses, and Seychelles decrease rapidly due to warming. Ocean acidification will lower the habitat suitability in reef locations, and negative impacts of ocean acidification will outweigh the positive impacts of warming (chapter 4).

6. Changes in temperature and salinity, temperature and phosphate, temperature and $\Omega_{\text{ara}}$, salinity and $\Omega_{\text{ara}}$, phosphate and $\Omega_{\text{ara}}$ affect coral reef suitability non-linearly. In contrast, the combined effects of changing nitrate with other factors (i.e. temperature, salinity, phosphate, $\Omega_{\text{ara}}$) and salinity with phosphate are additive (chapter 5).

In summary, this work has contributed to a better understanding of global coral reef distribution by (a) exploring the impacts of environmental change on distributions of potential reef habitat and (b) estimating the reef habitat suitability in relation to global warming and ocean acidification. The coral reef tolerance limits to environmental variables are updated from previous limits. The parametric function of reef habitat suitability is the first attempt to quantify the fitness of global coral reefs and explicitly explore the fitness of coral reefs with respect to climate change. The novelty of the results presented in this thesis, thus, lies in the application of the new tolerance limits of coral reefs (chapter 2) to predict distribution of potential reef habitats and application of the habitat suitability response function (chapter 3) to predict habitat suitability change (chapters 3 and 4).
Appendices

A. Chapter 2 Supporting information

Mismatch between bottom topography and coral reef data

The projection of the coral reef distribution data onto the most recent bottom topography reveals an important discrepancy between the bathymetry data (GEBCO_08) and the charted coral reef locations the Global Distribution of Coral Reefs (2010) (IMaRS-USF & IRD, 2005; IMaRS-USF, 2005; UNEP-WCMC, WorldFish Centre, WRI and TNC, 2010). The depth at the charted coral reef locations is frequently found to be deeper than 2000 m and up to 7000 m, which is obviously incorrect for tropical warm water corals. As an example, Moorea Island is a high island in French Polynesia, 17 km northwest of Tahiti, located in the archipelago of the Society Islands in the southern Pacific Ocean. The coral reefs at the eastern shore of the small island correspond to very deep waters (see Figure A 1). A similar mismatch occurs in many atolls of French Polynesia and at any location where the GEBCO_08 bathymetry results, despite its high resolution of 30” x 30”, is rather coarse.

The GEBCO_08 Grid with 30 arc-second resolution is up to date the most accurate bottom topography available and much more accurate than ETOPO1 or ETOPO5 with 1 arc-minute and 5 arc-minute resolutions, respectively. However, the GEBCO_08 bathymetry is created from a combination of ship based echo sounder data and satellite derived gravimetric data, wherever no ship data are available, which is often the case in remote and scarcely populated ocean regions like Oceania. An ocean basemap reconstructed on the basis of satellite gravimetric data will never be so accurate as to resolve coral reef structures and more ship based measurements are required to refine available topography datasets. In addition, errors may also affect the bathymetry data, like islands in the dataset that simply do not exist in reality (Seton et al., 2013).

Given these uncertainties in the available bathymetry data we performed a sensitivity analysis for different minimum light intensities to estimate the most suitable light level for coral growth, as described in the main text.
Figure A.1 Coral reef distribution (orange) around Moorea Island (17.53°N, 149.83°W) and Tahiti Island (17.67°N, 149.42°W) overlaid on the GEBCO_08 Grid bathymetry.
Note the portions of reefs erroneously lying over very deep waters (dark blue spots).

**Figure A.2** The distribution of false positives (left panels) and false negatives (right panels) obtained by running ReefHab with the K97 limits and with $I_{\text{min}} = 300$ $\mu$mol photons m$^{-2}$ s$^{-1}$ for each environmental variable. The maps are on a $1^\circ \times 1^\circ$ spatial resolution. Only considering temperature, given the definition of false positive, the red grid cell in false positive for temperature represents the area within the tolerance limits we set for potential reef habitats, but no observed reef found in that area. False positives contribute to overestimation of reef areas, for example, in Mediterranean Sea where there are non-reef corals. The same way of interpreting the information for false negative, red grid cells contribute underestimation of observed reef, for example, due to unsuitable phosphate tolerance, lots of reefs are not captured by ReefHab in Indo-Pacific region.
Figure A.3 False positives (left panels) and false negatives (right panels) obtained by running ReefHab with the new environmental tolerance limits (this study) and with $I_{\text{min}} = 450 \ \mu\text{mol photons m}^{-2} \ \text{s}^{-1}$. The same way of interpreting the information as in S2 Fig. 1. Noticeably, the GLDAP dataset for DIC and TA does not cover the Indonesian Sea and the Caribbean. We created a mask for these two regions, when ReefHab checks these two regions, only temperature, salinity, nitrate, phosphate, and light condition are considered.
Figure A.4 Total 51 false positives obtained by running ReefHab combined with all the new environmental tolerance limits (this study) and with $I_{\text{min}} = 450$ μmol photons m$^{-2}$ s$^{-1}$.

B. Chapter 3 Supporting information

Figure B.1 Derivatives of the regional suitability index (green lines) with respect to a bin size change in each environmental variable. The bin sizes of the histograms for each variable are calculated using the Freedman-Diaconis’ rule (see Methods). The bin sizes for SST, $\Omega_{\text{sea}}$, NO$_3$, and PO$_4$ are, respectively, 0.1°C, 0.02, 0.02 μmol L$^{-1}$, and 0.01 μmol L$^{-1}$. The red lines are the regional normalized frequency distributions of reef occurrences for the various environmental variables. The parameters ($\xi$, $\alpha$, $\omega$, and $\kappa$) of the frequency distributions are reported in Supplementary Table S1.
Figure B.2 Histograms of reef occurrences and frequency distributions (red lines). The bin size of the histograms are 0.1°C for SST, 0.02 for \( \Omega_{\text{ara}} \), 0.02 μmol L\(^{-1}\) for NO\(_3\), and 0.01 μmol L\(^{-1}\) for PO\(_4\) and are calculated using the Freedman-Diaconis' rule (see Methods). In GBR, most of the reefs are found in locations characterised by an \( \Omega_{\text{ara}} \) below about 3.4 and the regional optimum is 3.3 (Table 1). The statistical parameters (\( \xi, \alpha, \omega, \) and \( \kappa \)) of the frequency distributions are reported in Supplementary Table S1.

Figure B.3 Locations (blue dots) with negative impacts caused by both warming (+0.1 °C) and decreasing \( \Omega_{\text{ara}} \) (-0.02).
The table below shows the statistical parameters for global and regional normalized variances in relation to different environmental variables.

<table>
<thead>
<tr>
<th>Variable</th>
<th>No.</th>
<th>Mean</th>
<th>Median</th>
<th>25th</th>
<th>50th</th>
<th>75th</th>
<th>90th</th>
<th>95th</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pacific Ocean</td>
<td>2857</td>
<td>0.96</td>
<td>0.01</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>Caribbean Region</td>
<td>28.14</td>
<td>0.96</td>
<td>0.01</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>Gulf of California</td>
<td>27.53</td>
<td>0.96</td>
<td>0.01</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>Red Sea &amp; Gulf of Aden</td>
<td>27.07</td>
<td>0.96</td>
<td>0.01</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>Atlantic Ocean</td>
<td>2658</td>
<td>0.96</td>
<td>0.01</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
</tr>
</tbody>
</table>

**Note:** The table includes statistical parameters for global and regional normalized variances, with mean, median, 25th, 50th, 75th, 90th, and 95th percentiles.
Table B.2 Geographical information of the six regions and number of reef locations found in each region. The total number of reef locations in the six regions is 25270, 85% of the global reef cover (accounting for 29550 reefs).

<table>
<thead>
<tr>
<th>Region</th>
<th>Latitude</th>
<th>Longitude</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Southeast Asia</td>
<td>12°S-18°N</td>
<td>90°E-137°E</td>
</tr>
<tr>
<td>2. Great Barrier Reef</td>
<td>10°S-28°S</td>
<td>140°E-157°E</td>
</tr>
<tr>
<td>3. Great Caribbean Region</td>
<td>5°N-35°N</td>
<td>55°W-100°W</td>
</tr>
<tr>
<td>5. Western Indian Ocean</td>
<td>30°S-8°N</td>
<td>30°E-75°E</td>
</tr>
<tr>
<td>6. Central Pacific</td>
<td>28°S-16°N</td>
<td>158°E-117°W</td>
</tr>
</tbody>
</table>
C. Chapter 4 Supporting information

Figure C.1 SST at reef locations.

Figure C.2 Isolines of SST at 21.7 °C in 2010 (red solid line) and in 2090 (blue solid line). The 21.7 °C is the lower tolerance limit of coral reefs. The isoline of $\Omega_{ara}$ at 2.82 in 2010 (blue dashed line) and in 2090 (green dashed line).
Figure C.3 $\Omega_{ara}$ at reef locations.

D. Chapter 5 Supporting information

Figure D.1 Reef occurrences as functions of single environmental factors. The optimal conditions correspond to 28.6°C for T, 34.8 psu for S, 0.06 μmol L⁻¹ for N, 0.2 μmol L⁻¹ for P, and 3.8 for Ω.
Figure D.2 Reef occurrences as a function of factor A (columns, with factor values given on X-axis) at different levels of factor B (rows, values shown in insets). Factor labels are given in the diagonal. The Y-axis indicates numbers of reef occurrences.
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