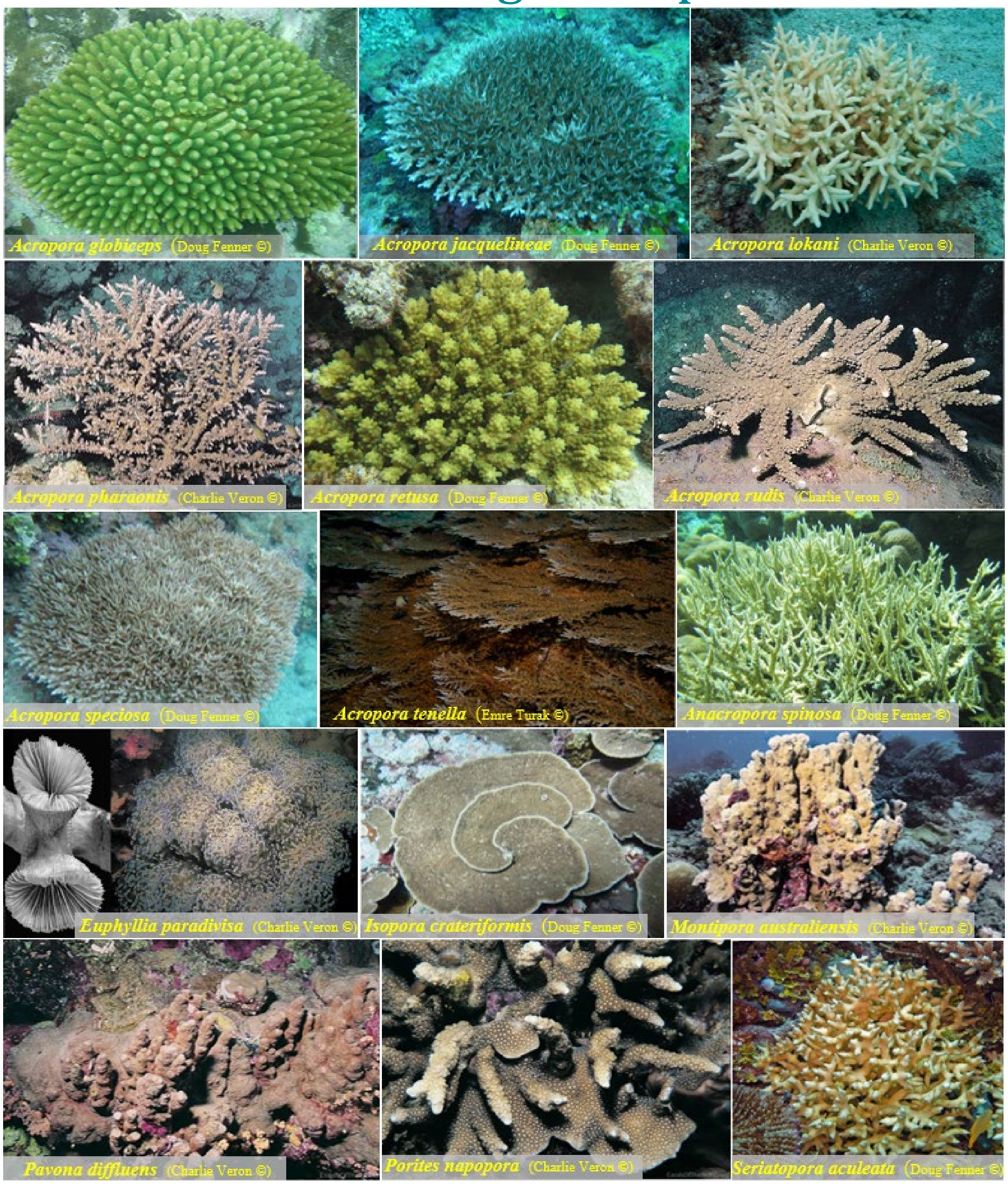
Recovery Status Review for 15 Species of Indo-Pacific Reef-building Corals Listed under the Endangered Species Act



July 2023, Pacific Islands Regional Office

NOAA National Marine Fisheries Service

Contents

Executive Summary

This Recovery Status Review (RSR) is intended to inform the development of a recovery plan for the 15 Indo-Pacific reef-building coral species listed as threatened under the Endangered Species Act (ESA) in 2014 and the ecosystems upon which they depend. To that end, key ecosystem trends are first described to provide context, followed by a general evaluation of the most important threats to Indo-Pacific reef-building corals, and finally species reports for each of the 15 listed corals. The RSR provides the information needed to formulate actions in the recovery plan.

Over the past few decades, disturbances of Indo-Pacific coral reef ecosystems have become more frequent and severe especially warming-induced coral bleaching events while the available recovery times have become shorter. These patterns have diminished overall resilience despite the large size, high biodiversity, and substantial proportion of remote areas of Indo-Pacific coral reef ecosystems. Coral cover has declined in most regions, compounded by replacement of sensitive coral species with hardier species and reductions in diversity. Overall, the observed trends in the extent of disturbance, recovery time, overall resilience, coral cover and community composition collectively illustrate a steady decline in Indo-Pacific coral reef ecosystems in recent decades, and these trends are expected to continue and worsen in the foreseeable future unless the most important threats are brought under control.

The main threats to Indo-Pacific reef-building corals including the 15 listed species have worsened since listing in 2014, especially the most important threat, ocean warming and warming-induced bleaching. All threats are projected to become much more severe throughout the 21st century if current levels of greenhouse gas (GHG) emissions continue, which would lead to global warming above pre-industrial levels of nearly 3° C. Even if the goal of the 2016 Paris Agreement is met and global warming is limited to 1.5° C above pre-industrial, ocean warming, ocean acidification and sea-level rise will likely continue to worsen throughout the 21st century, while local threats such as unsustainable fishing and land-based sources of pollution are likely to also worsen as the human population and economic development increase. That is, additional regulatory mechanisms for the management of both climate change and local threats are necessary to halt the decline of reef-building corals including the 15 listed species let alone provide for their recovery.

Of the 15 listed corals, 11 species are in the Acroporidae family (*Acropora globiceps, A. jacquelineae, A. lokani, A. pharaonis, A. retusa, A. rudis, A. speciosa, A. tenella, Anacropora spinosa, Isopora crateriformis, Montipora australiensis*) while the four others are each in different families (*Euphyllia paradivisa, Pavona diffluens, Porites napopora,* and *Seriatopora aculeata*). The 15 species were listed mainly because of their limited distributions, low and declining abundances, high susceptibilities to ocean warming, ocean acidification, and other important threats, and high likelihood that the most important threats will substantially worsen in the foreseeable future (i.e., now to 2100). Since 2014, all threats have become more severe, especially ocean warming, as illustrated by the series of marine heatwaves and coral bleachings across the Indo-Pacific since then.

Based on the information in the RSR and cited documents, global and local threats to the 15 listed species are worsening, especially the most important threat, ocean warming and warming-induced coral bleaching. All threats are projected to become much more severe in the foreseeable future. Recovery of the 15 species is not possible unless the worsening trends are at least stabilized, especially for the threats resulting from global climate change, ocean warming and ocean acidification. That is, a viable recovery strategy must be based on controlling global climate change.

Figures

Tables

1. Introduction

1.1. Scope and Intent of the Present Document

In 2009, the Center for Biological Diversity (CBD) petitioned the National Marine Fisheries Service (NMFS, also known as NOAA Fisheries) to list 75 Indo-Pacific reef-building coral species as threatened or endangered under the United States (U.S.) Endangered Species Act (ESA; CBD 2009). CBD selected the 75 species with 2 criteria: (1) occurrence in U.S. waters, based on information available at that time; and (2) inclusion on the International Union for Conservation of Nature's Red List of Threatened Species. That is, the petition was limited to U.S. reef-building coral species at relatively high extinction risk, and was not necessarily representative of Indo-Pacific reef-building corals with the highest extinction risk globally.

In response to the petition, NMFS completed a Status Review Report (SRR) for the 75 petitioned species in 2011 (Brainard et al. 2011), and listed 15 of the 75 species as threatened under the ESA in 2014. These species are *Acropora globiceps, A. jacquelineae, A. lokani, A. pharaonis, A. retusa, A. rudis, A. speciosa, A. tenella, Anacropora spinosa, Euphyllia paradivisa, Isopora crateriformis, Montipora australiensis, Pavona diffluens, Porites napopora,* and *Seriatopora aculeata*, as described in the final listing rule (79 FR 53851).

The decision about whether or not to list a species as threatened or endangered under the ESA requires determination of the status of the species currently and over the foreseeable future (ESA section 4). However, Indo-Pacific reef-building corals have many biological and habitat features that complicate the determination of the status of any given species, including but not necessarily limited to: most are modular, colonial, and sessile; the definition of the individual is ambiguous; the taxonomy of many species is uncertain; field identification of many species is difficult; colonies or polyps are a collection of coral-algae-microbe symbiotic relationships; skeletal plasticity is high within many species; they utilize a combination of sexual and asexual reproduction; hybridization may be common in many species; high habitat heterogeneity fosters acclimatization and adaptation to wide ranges of environmental conditions; and large ranges encompass habitats that provide refuges from disturbances (e.g., Osman et al. 2018, Sully and van Woesik 2020, Dietzel et al. 2021). These factors were considered in the final listings of the 15 listed corals (79 FR 53851), the Not Warranted determinations for the 60 other petitioned species (79 FR 53851), and the Not Warranted determination for *Pocillopora meandrina* (NMFS 2020) in response to a petition to list that species (CBD 2018).

For marine species listed under the ESA, NMFS must develop and implement recovery plans, unless they will not have conservation benefit to the species (ESA Section 4(f)(1)). The purpose of a recovery plan is to provide a roadmap for a species' recovery, with the goal of improving its status and managing threats to the point at which protections under the ESA are no longer needed.

1.2. Approach to the Recovery Status Review

This document is a Recovery Status Review (RSR) for 15 Indo-Pacific coral species. It contains information on the species' biology and status to inform ESA actions, and can be updated periodically as new information becomes available. This RSR is the most comprehensive and current source for the 15 coral species' biological and status information needed for many ESA decisions (e.g., section 7 consultations, grants, permits, conservation plans developed under Section 10, 5-year reviews, and recovery planning). The RSR includes background on Indo-Pacific reef-building corals and the 15 listed species (Section 2), a general threats evaluation (Section 3), and species reports for the 15 listed species (Section 4). The RSR is based largely on the original SRR (Brainard et al. 2011), the Management Report that describes relevant regulatory mechanisms and conservation efforts (NMFS 2012), the final listing rule for the 15 listed species (79 FR 53851), and the general status review conducted as part of the response to the petition to list for *Pocillopora meandrina* (Smith 2019), updated with more recent information from the scientific and gray literatures.

While the information in this document is not a full compilation of unabridged text from the other aforementioned sources, it is also more than a mere summary. However, original sources (e.g., SRR, final listing rule, etc.) contain more exhaustive descriptions of certain topics, and like any reference cited, should be referred to for more contextual information, where appropriate or where noted. For example, the SRR (Brainard et al. 2011) contains much more detailed information on general coral reef ecology and general reef-building coral biology from the classic scientific literature than this document. The SRR (Brainard et al. 2011), final listing rule (79 FR 53851), and related documents are available for download at https://www.fisheries.noaa.gov/corals.

A Recovery Status Review does not result in any decisions. Rather, it provides the best scientific and commercial data available to inform management and recovery actions for ESA listed species.

2. Background on Indo-Pacific Reef-building Corals

Reef-building corals are defined by symbioses with unicellular photosynthetic algae living within their tissues (zooxanthellae), hence they are sometimes referred to as “zooxanthellate” or “hermatypic” corals. The symbiosis provides them the capacity to grow large skeletons and thrive in nutrient-poor tropical and subtropical seas. Reef-building corals collectively produce shallow coral reefs over time, and over 90% of the world’s coral reefs occur in the Indian and Pacific Oceans (i.e., the Indo-Pacific, Brainard et al. 2011, 79 FR 53851). Recent and projected ecosystem trends are key in determining the status of the listed corals and thus are summarized in this section, together with a description of coral species distributions and background on the 15 listed corals.

2.1. Key Ecosystem Trends

The status of reef-building corals is largely determined by the extent of disturbance, the amount of time available to recover from disturbance, and overall resilience of the reef-building coral communities and coral reef ecosystems. The most common measure of the status of Indo-Pacific reef-building coral communities is live coral cover of all species combined. Coral cover does not typically consider community composition (e.g., diversity of coral species), which is an important measure of coral community health. Trends in the extent of disturbance, recovery time, overall resilience, and coral cover and community composition are summarized below. These trends are described both in terms of observations since relevant scientific information became available (≈1950), and projections over the foreseeable future (i.e., from now to 2100; 79 FR 53851, NMFS 2020).

Extent of Disturbance. Disturbance is defined as an anthropogenic or natural event that results in large-scale coral colony mortality. All of the threats described in the Threats Evaluation below are at least partially anthropogenic, and have the potential to cause large-scale disturbance. Disturbances may be acute (shorter-term, more intense) or chronic (longer-term, less intense) (Connell 1997). Natural disturbance is key for maintaining high diversity of reef-building corals in coral reef ecosystems. That is, over a given time period, variable conditions throughout cycles of disturbance and recovery at a given reef site enable a higher diversity of species to occur at that site than in the absence of disturbance (Hughes and Connell 1999). Observed and projected disturbance of Indo-Pacific reef-building coral communities are described below.

Overall, observed acute and chronic disturbances of Indo-Pacific coral reefs have sharply increased over the past several decades (Brainard et al. 2011, Birkeland 2019, Hughes et al. 2021). As described in the Ocean Warming section of the Threats Evaluation (Section 2.2.1), the most important pattern in observed disturbance of Indo-Pacific coral reefs is the increase in the frequency, intensity, and magnitude of large-scale, warming-induced coral bleaching events. The repeated bleachings of 2014 – 2017 together constitute the most severe coral bleaching event ever recorded in the Indo-Pacific, and affected many remote reefs far from local human impacts (Eakin et al. 2017, Hughes et al. 2017a, Hughes et al. 2018a). Ocean acidification represents a chronic disturbance because of its continual effects on both coral calcification and reef accretion. Both ocean acidification and its impacts on corals have been observed to be increasing in the Indo-Pacific (Iida et al. 2020, Davis et al. 2021). Localized chronic disturbances such as land-based sources of pollution (Carlson et al. 2019, Donovan et al. 2021) and coral disease outbreaks (Aeby et al. 2020, Howells et al. 2020) are all broadening and worsening on coral reefs near human populations throughout the Indo-Pacific.

As described in the Threats Evaluation (Section 3), all threats to Indo-Pacific reef-building corals are projected to increase in the foreseeable future. In addition, the interactions of threats with one another are likely to become more severe in the foreseeable future than currently. These threats collectively are projected to result in increases in the frequency, intensity, and magnitude of both acute and chronic anthropogenic disturbances of Indo-Pacific reef-building coral communities in the foreseeable future. Spatial variability in all disturbances combined is expected to be high across the region, as some areas are more susceptible to multiple, simultaneous threats and their subsequent disturbances than others. However, areas that currently provide refugia from threats are likely to shrink under conditions projected during the 21st century (van Hooidonk 2014, 2016, 2020).

Recovery Time. Recovery time refers to the amount of time needed for a reef-building coral community to be restored after a disturbance to a degree comparable to its original state (Pearson 1981, Birkeland 2019). Reviews of the impacts of disturbance on Indo-Pacific coral communities have found that recovery of coral cover alone generally took less than 10 years in the absence of additional disturbances, where most recovery was due to rapid regrowth of fast-growing branching or tabletop *Acropora* species (Connell 1997, Baker et al. 2008). However, this type of recovery typically results in a less diverse coral community with fewer slow-growing reef-building coral species than pre-disturbance (Berumen and Pratchett 2006). Most studies of recovery of both coral cover and community structure have concluded that recovery from an acute disturbance usually takes about 10 – 15 years, as long as there are no additional chronic or acute disturbances (Birkeland 2019). However, as disturbances have increased in frequency, intensity, and magnitude, the amount of recovery time available has steadily decreased over the past several decades (van Hooidonk et al. 2016, Hughes et al. 2021).

As described in more detail in the Threats Evaluation, all threats are projected to increase in the foreseeable future, leading to higher frequency, intensity, and magnitude of both acute and chronic anthropogenic disturbances of Indo-Pacific coral reefs. One of the most important implications of the projected increasing frequency of disturbance is the subsequent reduction in recovery time. For example, an analysis of the timing of Annual Severe Bleaching (ASB) of the world's coral reefs in the 21st century concluded ASB will occur on >75% of all reefs by mid-century, essentially eliminating the time available for recovery on those reefs, assuming no capacity for acclimatization or adaptation of corals to higher temperatures (van Hooidonk et al. 2016). Although the spatial variability of conditions on Indo-Pacific coral reefs provides networks of refugia from threats, the increasing prevalence of all types of disturbance will likely erode or eliminate many of these refugia. Thus, the ever-increasing frequency of disturbance is projected to reduce the capacity of coral reefs to recover through reduction of recovery times (Hoegh-Guldberg et al. 2017, Skirving et al. 2019, Hughes et al. 2021), especially under "business-as-usual" climate change scenarios (Heron et al. 2017, van Hooidonk et al. 2020).

Overall Resilience. Overall resilience is a broader concept than recovery and is defined as the capacity of reef-building coral communities and coral reef ecosystems to recover from disturbance without undergoing a phase shift (i.e., transition from a coral-dominated system to an algae-dominated system), maintaining their original state through disturbance, or reversing to their original state after a phase shift. Thus, overall resilience has three major components: (1) Recovery, defined as an individual, population, or community returning to its original state after disturbance; (2) resistance, defined as the ability to be unaffected or lightly affected by disturbance; and (3) reversibility, defined as the ability to shift back to the original state after a phase shift. Resilience applies to the individual (colony), population, and community levels, here termed "overall resilience." Loss of resilience is indicated both by the inability to recover, leading to a phase shift, and the inability to reverse a phase shift. Such loss of resilience has been widely observed in Caribbean coral reefs but less so in Indo-Pacific coral reefs because: (1) The Caribbean has inherent characteristics that provide relatively less resilience than the Indo-Pacific, such as relatively small ecosystem size, lower fish and coral diversity, and lower abundances of herbivores; and (2) human impacts in the Caribbean are generally higher than in the Indo-Pacific, resulting in relatively more coral reef degradation and higher proportions of imperiled foundational reef-building coral species (Jackson et al. 2014, Roff et al. 2015, NASEM 2019).

Several factors confer overall resilience to Indo-Pacific reef-building communities and ecosystems, including high habitat heterogeneity, large ecosystem size, and high coral and reef fish species diversity (Roff and Mumby 2012, 79 FR 53851). Relatively high overall resilience is indicated by: (1) observed impacts of disturbances on corals have been spatially highly variable (Hock et al. 2017, Guest et al. 2018); (2) observed responses of corals to disturbances show that most either were resistant or recovered given adequate recovery time (Connell 1997, Baker et al. 2008, Birkeland 2019); and (3) observed responses of coral reefs to disturbances show that phase shifts have been either rare or reversed (Cheal et al. 2010, Graham et al. 2013). However, the limits of overall resilience are being exceeded by the ever-increasing frequency, intensity, and magnitude of disturbance and subsequent reduction in recovery times (Birkeland 2019, Hughes et al. 2021), even on remote reefs (Smith et al. 2017, Baumann et al. 2021). As described in the Threats Evaluation below, all major threats to Indo-Pacific reef-building corals are projected to increase throughout the 21st century, including the most important threat of ocean warming and warming-induced bleaching. Consequently, disturbance and bioerosion are projected to increase, and recovery times and coral cover are projected to decrease. Thus, overall resilience for Indo-Pacific reef-building coral communities and coral reef ecosystems is projected to decline in the foreseeable future.

Coral Cover and Community Composition. Coral cover is defined as the percentage of the seafloor occupied by living reef-building corals, and is an important metric of coral reef health (Jones et al. 2004, Dustan et al. 2013). A collection of anecdotal accounts by early coral reef researchers describes high coral cover on reef flats and reef slopes in French Polynesia, the Great Barrier Reef (GBR), Thailand, Madagascar, east Africa, and the eastern Pacific from the 1950s to the 1970s (Sale and Szmant 2012). Anthropogenic disturbance resulted in coral cover declines before coral reef monitoring programs began in the 1960s and 1970s, and prior to more recent threats such as warming-induced bleaching and ocean acidification (Pandolfi et al. 2003). In the 1960s, researchers started collecting coral cover data at some locations in the Indo-Pacific, providing the first quantitative descriptions of coral cover in the region (e.g., Gomez et al. 1981). More extensive reef monitoring programs began in the late 1970s and spread throughout the region in the following decades, providing time-series of coral cover data from many locations that can provide insight on temporal trends (e.g., Bruno and Selig 2007, Atewerberhan et al. 2011, Brainard et al. 2012, De'ath et al. 2012, Magdaong et al. 2013).

The Global Coral Reef Monitoring Network (GCRMN) was established in 1995 to coordinate the consolidation and reporting of coral monitoring results, producing global reports starting in 1998 and most recently in 2020 (GCRMN 2020). GCRMN organizes the coral reefs of the world into 10 regions, 8 of which are in the Indo-Pacific. GCRMN's 2020 report summarizes coral reef monitoring data from 1979-1998 (depending on region) to 2019 for each of the 10 regions, based on 34,870 surveys at 12,160 sites. Mean annual live hard coral cover results for the eight Indo-Pacific regions are shown in Figure 1. Major bleaching events occurred in 1998, and several times between 2010 and 2019. Most regions had overall decreases in coral cover, especially after the worst bleaching events in 1998 and 2016. Recoveries occurred in most regions during the decade following the 1998 event. However, from 2010 to 2019, all regions had decreases in coral cover, although there was high variability between and within regions (GCRMN 2020).

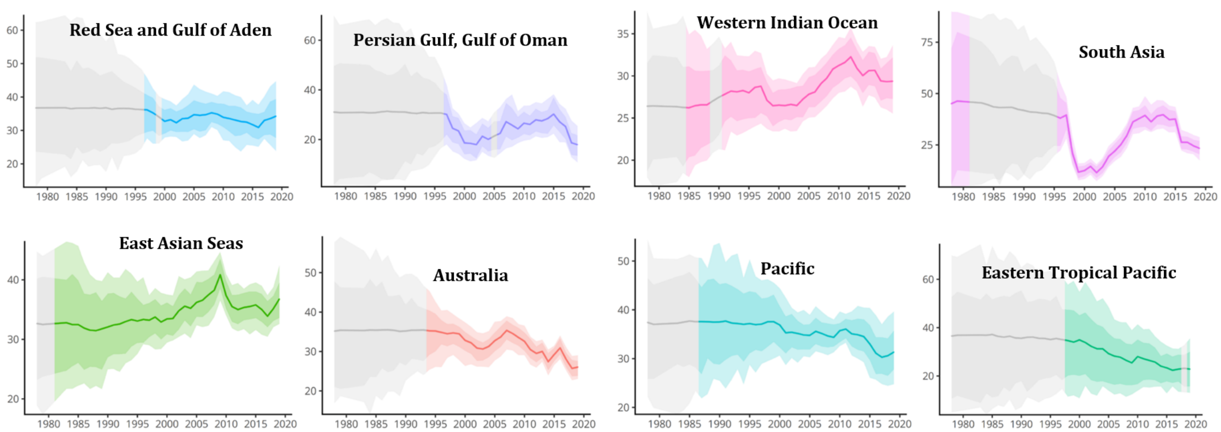


Figure 1. Coral cover monitoring results from the eight GCRMN Indo-Pacific regions through 2019 (GCRMN 2020, Chapters 3 – 10). Hard coral cover (%) is shown on the X axes. The solid lines represent the estimated means. The associated darker and lighter shades represent the 80% and 95% confidence intervals, respectively. Grey areas represent periods during which no data were available.

The monitoring results confirm that warming-induced coral bleaching is the greatest threat to the world's reef-building corals, approximately 90% of which are in the Indo-Pacific. The 1998 bleaching event alone killed 8% of the world's reef-building coral, and bleaching events since 2010 have killed 14% (GCRMN 2020). Given the ocean warming projections described in Section 3.2.1, coral cover is projected to substantially decrease over the foreseeable future. Observed and projected impacts to reef-building corals may be even worse than indicated by coral cover, because coral cover alone does not account for changes in coral community composition.

Coral cover is the simplest measure of the condition of reef-building coral communities, but may overlook changes in coral community composition such as changes or reductions in coral species diversity (Hughes et al. 2012), as shown by these three examples: Historical reconstructions of inshore GBR reefs showed that communities dominated by large colonies of thick-branched *Acropora* species collapsed between 1920 and 1955 in response to chronic increases in sediments and nutrients following European settlement around 1870. In recent decades at one of the sites, coral cover recovered to levels similar to or greater than historic levels, but with relatively hardy *Pavona* species replacing *Acropora* species as the dominant taxa (Roff et al. 2013). A study of a Moorea reef documented how the *Acropora* community was decimated in 1981 by the crown-of-thorns seastar (COTS). Subsequently, *Pocillopora* species became dominant, and coral cover of the

Pocillopora-dominated community in 2003 was slightly higher than that of the *Acropora*-dominated community in 1979 (Berumen and Pratchett 2006). The Australian Institute of Marine Sciences' (AIMS) Long-Term Monitoring Program has been collecting coral cover data on the GBR annually since 1987. Coral cover was higher in 2022 than at any time in the 36-year history of the program, after recovery from recent bleaching events. However, communities in 2022 were dominated by small colonies of fast-growing *Acropora* species that are highly susceptible to disturbance (AIMS 2022). In all three examples, changes in coral cover alone may imply that coral communities had "recovered," masking the changes in community composition.

Even when coral cover recovers to pre-disturbance levels, coral community composition may be affected in important ways, such as the replacement of sensitive species by hardier species, or reductions in coral species diversity, both of which may affect rare species such as the ESA-listed corals. But as described above from GCRMN (2020), coral cover is generally declining across the Indo-Pacific, which has even more serious implications for coral community structure. Since there is much more data on trends in coral cover than on community composition in the Indo-Pacific, it is unknown how much coral community composition has changed since the onset of the Industrial Era (circa 1850) or even over the past few decades as disturbances have rapidly increased. However, it is likely that Indo-Pacific coral community structure has been affected in various ways (Hughes et al. 2012), and that this trend will worsen in the foreseeable future in response to worsening threats.

<u>Ecosystem Trends Summary</u>. Over the past few decades, disturbance of Indo-Pacific coral reef ecosystems has become much more extensive, especially warming-induced coral bleaching events, while recovery times from the disturbances have become shorter. These patterns have diminished overall resilience despite the large size, high biodiversity, and substantial proportion of remote areas of Indo-Pacific coral reef ecosystems. Coral cover has declined in most regions, but trends in coral cover alone can be misleadingly optimistic because coral community composition is not typically monitored, in which case replacement of sensitive coral species with hardier species and reductions in diversity are not accounted for. Overall, the observed trends in the extent of disturbance, recovery time, overall resilience, and coral cover and community composition collectively illustrate a steady decline in Indo-Pacific coral reef ecosystems in recent decades. These trends are expected to continue and worsen in the foreseeable future, unless the most important threats are brought under control, as described in the Threats Evaluation below.

2.2. Coral Species Distribution and Abundance

The geographic distribution of the listed coral species is a key factor in determining their status. The best available information on the distributions of Indo-Pacific reef-building corals has long been provided by Charlie Veron's Corals of the World (COTW) books (Veron 2000) and website (Veron et al. 2016). Veron divides the coral reefs of the Indo-Pacific into 133 ecoregions, and the SRR (Brainard et al. 2011) and final listing rule (79 FR 53851) both determined the distributions of the listed species in terms of Veron ecoregions. However, this document uses Spalding et al.'s (2007) Marine Ecoregions of the World (MEOWs) to portray the geographic distributions of the 15 listed coral species. The switch from Veron ecoregions to MEOWs was made because mapping data and files are more readily available, and MEOW provinces are more useful for recovery planning.

The MEOW system divides the world's marine environments into 12 realms, 62 provinces, and 232 ecoregions. The collective ranges of the 15 listed corals occur in a total of 76 MEOWs across 26 provinces, as shown in Figure 2. The numbers of listed corals in each province are described and shown in Section 2.3, and the geographic distributions of each of the 15 listed corals provided in Sections 4.1 – 4.15 below.

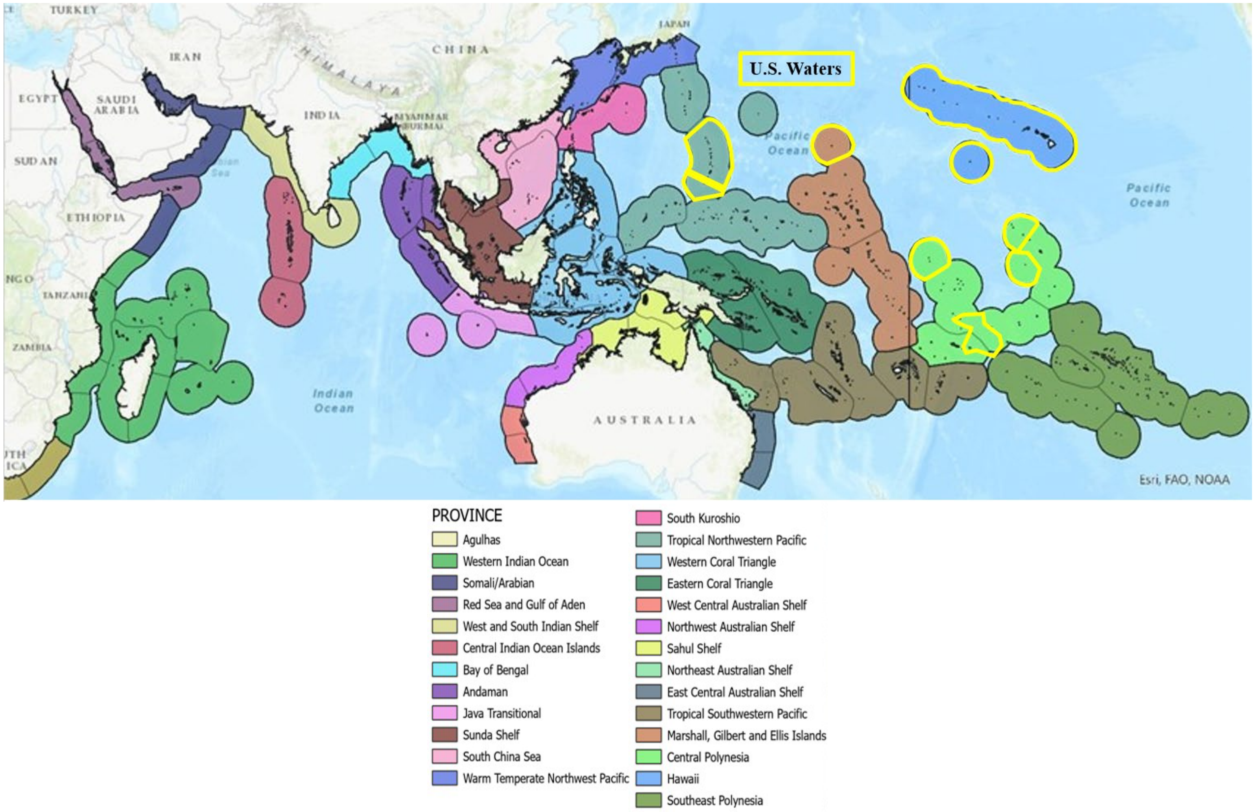


Figure 2. Collective geographic distributions of the 15 listed corals in the Indo-Pacific, based on the species-specific information in Section 4. The 15 species occur in 26 provinces and 76 ecoregions of Spalding et al.'s (2007) Marine Ecoregions of the World, including within U.S. waters as shown in yellow.

In addition to geographic distribution, the depth distribution of a species also influences their status. Unlike the geographic distributions of reef-building coral species provided in the COTW books (Veron 2000) and website (Veron et al. 2016), there is no comprehensive source of information on depth distributions. However, the Coral Traits Database (https://coraltraits.org/) provides depth distributions for many of the world's reef-building coral species.

Abundance of the listed coral species is also a key factor in determining their status. Abundance can be represented as relative abundance (i.e., how common a species is compared to others). While there is no comprehensive source for the relative abundances of reef-building coral species, DeVantier and Turak (2017) published a large study on the abundances of over 600 Indo-Pacific reef-building coral species in 31 of Veron 133 Indo-Pacific ecoregions, based on survey data collected from 1994 to 2016. Their results provide ecoregion-scale relative abundance data for all of the listed corals in terms of the following categories: Very Rare, Rare, Uncommon, Common, Very Common; and Near Ubiquitous (DeVantier and Turak 2017).

Abundance can also be represented as absolute abundance (i.e., the total number of colonies of a species that currently exists throughout its range). While there is no comprehensive source for the absolute abundances of reef-building coral species, several studies provide estimates for some species, including Dietzel et al. (2021) and Richards et al. (2008, 2019). Also, the final listing rule used distribution and relative abundance information to develop minimum absolute abundance estimates for the listed species (79 FR 53851).

The most informative abundance metric regarding the status of the species is its rangewide abundance trend over time. Such data are difficult to collect and there is no such information for any of the listed species. The final listing rule (79 FR 53851) assumed that based on the continued worsening of the most important threats, it is likely that the listed species are decreasing in overall abundance (i.e., abundance across all the ecoregions that make up a species' range).

2.3. The 15 Listed Species

The 15 Indo-Pacific reef-building coral species (Table 1) were listed as threatened under the ESA in 2014 based on the best available information at that time. The ESA defines a "threatened species" as "any species which is likely to become an endangered species within the foreseeable future throughout all or a significant portion of its range." (ESA Section 3(20)). The time period from the present to 2100 is interpreted as the foreseeable future for these species (79 FR 53851). We determined in 2014 that these species warranted listing as threatened under the ESA because their combinations of characteristics (i.e., limited geographic/depth distributions, relatively low abundances, and/or higher susceptibilities to key threats) together with future projections of threats indicated they are likely to be in danger of extinction within the foreseeable future throughout their ranges (79 FR 53851). We also determined that the other 60 petitioned Indo-Pacific corals (CBD 2009) did not warrant listing under the ESA because their characteristics (i.e., broad geographic/depth distributions, relatively high abundances, and/or lower susceptibilities to key threats) would adequately limit vulnerability to the threats (79 FR 53851).

Since 2014, new information has become available on the distributions, abundances, and threats for the 15 listed species, which has been incorporated into the detailed species reports in Section 3 and summarized in Table 1 below. Since listing in 2014, most threats have worsened, including the threats that are most important to most listed species (ocean warming and ocean acidification), as described in Section 2. In January 2021, NMFS announced that we will conduct 5-year reviews of these 15 species to ensure that their listing classifications are accurate, based on the best currently available information (NMFS 2021).

Table 1. Current information on the distributions (geographic, depth, US), abundances (relative, absolute), and threats impacting status for the 15 listed species, summarized from Section 4.

Listed Species	**Distribution**			**Abundance**		**Threats Impacting Status[f]**
	Geo[a]	**Depth[b]**	**US[c]**	**Relative[d]**	**Absolute[e]**	
Acropora globiceps	39	0-20	Yes	Uncommon to Common	≥hundreds of millions	1-7,9
Acropora jacquelineae	15	10-50	No	Uncommon	≥tens of millions	1-7,9
Acropora lokani	14	8-50	No	Uncommon	≥tens of millions	1-7,9
Acropora pharaonis	19	2-44	No	Common	≥tens of millions	1-7,9
Acropora retusa	35	0-29	Yes	Rare to Uncommon	≥hundreds of millions	1-7,9
Acropora rudis	9	3-30	No	Uncommon	≥millions	1-7,9
Acropora speciosa	33	12-65	Yes	Common	≥tens of millions	1-7,9
Acropora tenella	23	6-110	No	Uncommon to Common	≥tens of millions	1-7,9
Anacropora spinosa	17	5-15	No	Uncommon	≥millions	1-7,9
Euphyllia[1] paradivisa	24	5-75	Yes	Uncommon	≥hundreds of millions	1-4,6,7,9
Isopora crateriformis	27	0-25	Yes	Uncommon to Common	≥tens of millions	1-7,9
Montipora australiensis	36	2-30	No	Rare to Uncommon	≥tens of millions	1-7,9
Pavona diffluens	9	5-20	No	Uncommon	≥millions	1-6,9
Porites napopora	19	3-17	No	Uncommon to Common	≥millions	1-6,9
Seriatopora aculeata	26	3-40	No	Common	≥tens of millions	1-7,9

1. Name changed to *Fimbriaphyllia paradivisa* (see Section 4.2.10). a. Geo = Geographic distribution in number of Marine Ecoregions of the World; b. Depth distribution in meters; c. US = confirmed in US waters after listing in 2014; d. Relative abundance within the species' range; e. Absolute abundance in colonies; f. i.e., threats with at least a Low-Medium importance rating (threat codes: 1 = ocean warming; 2 = ocean acidification; 3 = disease; 4 = fishing; 5 = land-based sources of pollution; 6 = predation; 7 = collection and trade; 8 = sea-level rise; and 9 = inadequate regulatory mechanisms). See RSR Section 4 for more information and sources.

As noted in Section 2.2 and shown in Figure 2 above, the 15 Indo-Pacific listed corals occur in 26 of Spalding et al.'s (2007) 62 global marine ecosystem provinces. As with Indo-Pacific reef-building coral species diversity in general (Veron 2000, Veron et al. 2015), the highest numbers of listed coral species are concentrated in the Coral Triangle (i.e., Philippines, Malaysia, Indonesia, Papua New Guinea, Solomon Islands), where 12 listed species occur in the Western and Eastern Coral Triangle Provinces (Fig. 3). Relatively high numbers of listed corals also occur in the Sunda Shelf (11 spp.), Tropical Southwestern Pacific (11 spp.), Tropical Northwestern Pacific (9 spp.), and Central Polynesia (8 spp.) Provinces. Also following general diversity patterns, the fewest listed coral species occur in peripheral provinces, such as the Agulhas (South Africa), West and East Australian Shelf, and Hawaii Provinces (1 sp. each, Fig. 3).

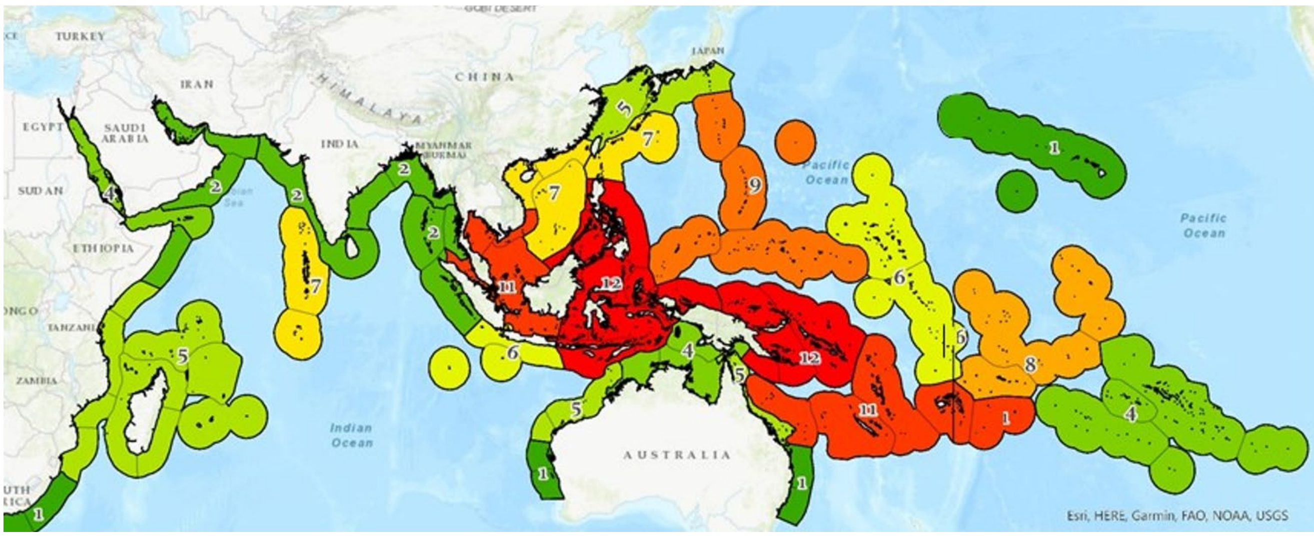


Figure 3. Numbers of listed corals in each of the 26 provinces (see Fig. 1), from most (12 species, bright red) to least (1 species, dark green), based on geographic distributions of each species described in Section 4.

3. Threats Evaluation

Section 4(a)(1) of the ESA and NMFS' implementing regulations (50 CFR 424) state that the agency must determine whether a species is endangered or threatened because of any of the following five factors:

(A) present or threatened destruction, modification, or curtailment of habitat or range;
(B) overutilization for commercial, recreational, scientific, or educational purposes;
(C) disease or predation;
(D) inadequacy of existing regulatory mechanisms; or
(E) other natural or manmade factors affecting its continued existence currently or in the foreseeable future.

The 2014 final listing rule (79 FR 53851) provided a general threats evaluation that defined and rated the most important threats to corals in general (i.e., the world's reef-building corals), as shown in Table 2 below (left columns), based on the SRR (Brainard et al., 2011). That threats evaluation was for the world's reef-building corals (i.e., Indo-Pacific and Atlantic combined), using the best available information at that time. Each threat was rated in terms of its relative importance to the extinction risk of corals in general (Table 1, 79 FR 53851). The general threats evaluation in this RSR is for Indo-Pacific reef-building corals only, based on currently available information, as also shown in Table 2 (right columns). The lack of species-specific information (i.e., for the 82 candidate corals in 2014 and the 15 listed corals currently) requires the use of general information to characterize threats to corals.

Differences in how threats are defined in the 2014 final listing rule vs. this RSR include: (1) fishing was limited to the trophic effects of fishing in the final listing rule, but includes both the trophic effects of fishing and habitat impacts from fishing in the RSR; and (2) sedimentation and nutrients were treated as separate threats in the final listing rule, but are combined into land-based sources of pollution in the RSR (Table 2). Differences in how the threats are rated in the 2014 final listing rule vs. this RSR include: (1) ocean warming was rated as High in the final listing rule but is rated as Very High in the RSR (2) ocean acidification was rated as Medium-High in the final listing rule but is rated as High in the RSR; (3) predation was rated as Low in the final listing rule but is rated as Low-Medium in the RSR; (4) collection and trade was rated as Low in the final listing rule but is rated as Low-Medium in the RSR; and (5) sea-level rise was rated as Low-Medium in the final listing rule but is rated as Low in the RSR (Table 2). In addition, the final listing rule did not rate the importance of the inadequacy of existing regulatory mechanisms, but the RSR provides a rating to clarify how this threat compares to the others. The rationales for these differences in how the threats are defined and prioritized in the RSR are provided in the specific threats descriptions in Section 3.2 and summarized in Table 2 below.

Table 2. Most important threats contributing to the extinction risk of: (1) the world's reef-building corals and their importance ratings based on the 2014 final listing rule (left); and (2) Indo-Pacific reef-building corals and their importance ratings based on information in this RSR, noting changes to the latter and references to RSR sub-sections for more information (right).

World's Reef-building Corals, 2014		**Indo-Pacific Reef-building Corals, 2023**	
Threat Definition	**Importance Rating**	**Threat Definition**	**Importance Rating**
Ocean Warming	High	No change	Changed to Very High, see Section 3.2.1.
Disease	High	No change	No change
Ocean Acidification	Medium-High	No change	Changed to High, see Section 3.2.2.
Trophic Effects of Fishing	Medium	Broadened to include habitat impacts from fishing, renamed "Fishing", see Section 3.2.4.	No change
Sedimentation	Low-Medium	Broadened to include nutrients and renamed "Land-based Sources of Pollution", see Section 3.2.5.	No change
Nutrients	Low-Medium	Broadened to include sedimentation and renamed "Land-based Sources of Pollution", see Section 3.2.5.	No change
Sea-level Rise	Low-Medium	No change	Changed to Low, see Section 3.2.8.
Predation	Low	No change	Changed to Low-Medium, see Section 3.2.6.
Collection and Trade	Low	No change	Changed to Low-Medium, see Section 3.2.7.
Inadequacy of Existing Regulatory Mechanisms	Not rated	No change	High

Ocean warming, ocean acidification, and sea-level rise are all direct results of increased concentrations of carbon dioxide (CO_2) and other greenhouse gases in the atmosphere. Because of its prominent role in driving two of the most important threats to reef-building corals, an overview of global climate change is provided in Section 3.1. This is followed by descriptions of each threat in Section 3.2, and the Threats Evaluation conclusion in Section 3.3. All threats except the inadequacy of existing regulatory mechanisms are described in terms of observed and projected effects to Indo-Pacific reef-building corals in general. "Observed" refers to the time period since relevant scientific information became available, while "projected" refers to the time period between now and the year 2100. The inadequacy of existing regulatory mechanisms is described in terms of their adequacy or lack thereof at managing threats. Species-level information on the impacts of the threats on each of the 15 listed species is described in Section 4.

3.1. Global Climate Change

The most important threats contributing to the extinction risk of Indo-Pacific reef-building corals result from global climate change. Global climate change refers to increased concentrations of greenhouse gases (GHGs; CO_2, methane, nitrous oxide, and others, of which CO_2 makes up approximately 80% of the total) in the atmosphere from anthropogenic emissions, and subsequent warming of the earth, acidification of the oceans, rising sea-levels, and other impacts since the onset of the industrial era (circa 1850). Since that time, the release of GHGs from industrial and agricultural activities has resulted in atmospheric CO_2 concentrations that have increased from approximately 280 ppm in 1850 (IPCC 2018) to 419 ppm in 2022, according to NOAA's Earth System Research Laboratory (ESRL) station on Mauna Kea, Hawaii (https://www.esrl.noaa.gov/gmd/ccgg/trends/, accessed August 2022). The resulting warming of the earth has been unequivocal (IPCC 2013, 2018, 2021, NCEI 2022).

In order to provide context for the climate change-related threats to the 15 listed species (primarily ocean warming and ocean acidification), and to support climate change-related management actions in the recovery plan, this overview covers 3 key points: (1) Observed global warming since the pre-industrial period (1850-1900); (2) efforts to control GHG emissions; and (3) additional global warming projected by 2100.

1. Observed Global Warming Since the Pre-industrial Period. Global Mean Surface Temperature (GMST) refers to the mean of air temperatures observed at the earth's surface over both land and sea. GMSTs can be estimated for the period of 1850 to 1900 based on temperature data collected from around the world by the United Kingdom's Hadley Centre and the University of East Anglia's Climatic Research Unit, known as HadCRUT. Data from this period establishes the "pre-industrial" GMST baseline used for comparisons with subsequent temperature changes (Fig. 4). According to the HadCRUT data, between the pre-industrial period (1850–1900) and 2021, observed GMSTs increased by over 1°C (Fig. 4, HadCRUT 2022).

GMSTs have increased at an average rate of 0.08°C per decade since 1880 and over twice that rate (0.18°C/decade) since 1981. Since 2015, GMSTs have increased even more rapidly (NCEI 2022). Warming is generally higher over land than over the ocean, thus warming of the ocean lags behind warming of air at the earth's surface. Regardless of future emissions, warming from past anthropogenic GHG emissions since the pre-industrial period will persist for centuries to millennia, and will continue to cause further long-term changes in the climate system, such as sea-level rise, with associated impacts (IPCC 2013, 2018, 2021).

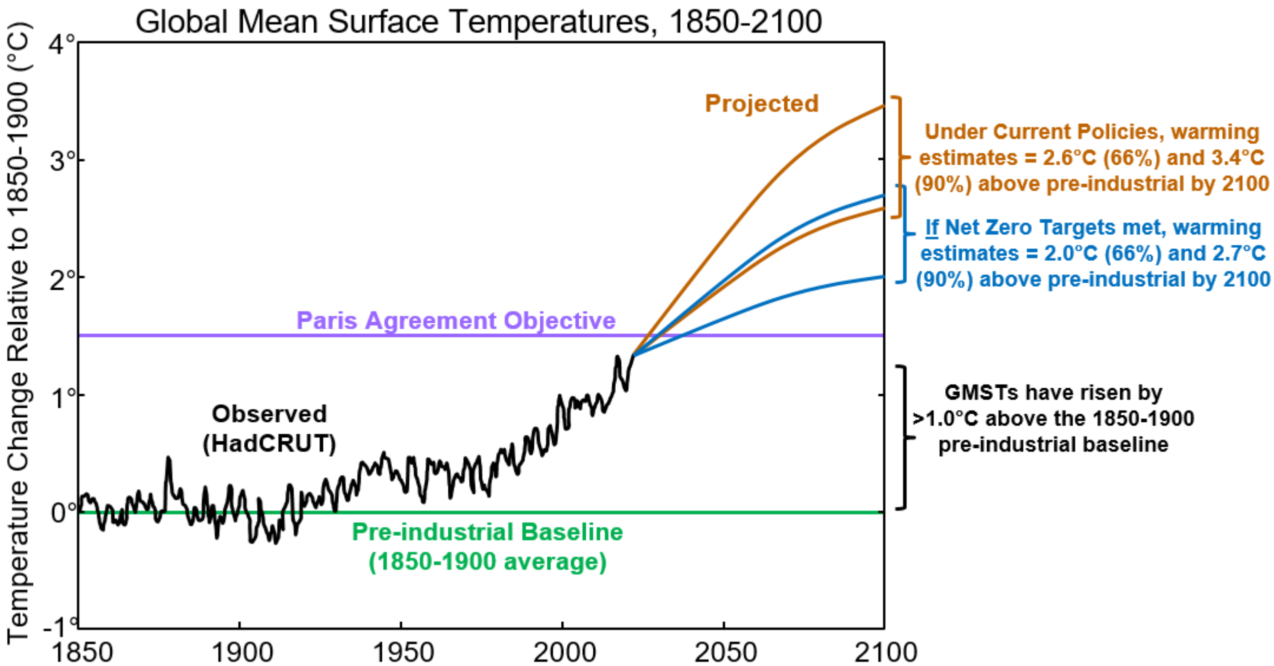


Figure 4. Global Mean Surface Temperatures (GMST), 1850-2100: Observed annual GMSTs from 1850 to 2021 (HadCRUT data, black line), relative to the pre-industrial baseline (green) and Paris Agreement objective (purple). Also shown are projected GMSTs to 2100 (66% and 90% likelihoods) resulting from current policies (brown) and successful implementation of net zero targets (blue), based on UNEP's 2021 Gap Report (UNEP 2021a).

2. Efforts to Control GHG Emissions. The necessity of limiting GHG emissions to control global warming was recognized many decades ago, leading to a series of international agreements, described in Section 2.3 below. GHG emissions are managed primarily through such agreements, which lead to statutes, regulations, and initiatives at the national, state, and local levels (UNEP 2018, 2019, 2020, 2021a). The most recent and extensive agreement is the 2015 Paris Agreement (UN 2015), which was signed in 2016 by 195 countries (UN 2016) with the objective of "holding the increase in the global average temperature to well below 2°C above pre-industrial levels and to pursue efforts to limit the temperature increase to 1.5°C above pre-industrial levels" (UN 2015, 2016). As shown in Figure 4, more than 1.0°C of global warming above the pre-industrial baseline has already occurred, thus meeting the 1.5°C objective of the Paris Agreement requires immediate and effective global action.

Each Paris Agreement signatory country is required to develop GHG reduction targets, then implement policies to meet the targets. The United Nations Environment Programme (UNEP) monitors the implementation of the Agreement via its annual Emissions Gap Reports (EGRs), which quantify the gap between the likely outcome of "current policies" of the Agreement's signatories vs. the Agreement's objective of limiting global warming to 1.5°C above pre-industrial by 2100 (i.e. the "emissions gap"). "Current policies" includes legislation and executive orders but not officially announced plans or strategies (UNEP 2021a).

3. Projected Additional Global Warming. The 2021 EGR provided 50%, 66%, and 90% likelihood estimates[1] of global warming by 2100 resulting from continuation of current policies, the 66% and

[1] In the UNEP Gap Reports, "likelihood" refers to the per cent chance that warming will be kept to X°C under scenario Y by date Z based on modeling results. For example, a 90% likelihood of 3.4°C of warming under current policies by 2100

90% results of which are used in this document. Projected global warming estimates by 2100 resulting from continuation of current policies (as of December 2021) are 2.6°C (66%) and 3.4°C (90%)[2] above the pre-industrial baseline (Fig. 4, UNEP 2021a). Error ranges for the 66% and 90% likelihood estimates are provided in footnote #2 below.

As noted above, current policies do not include announced plans or strategies. However, an important, recent development in GHG management is the commitments by over 100 countries to reduce their net GHG emissions to zero by 2050, i.e., "net zero targets." Projected global warming estimates by 2100 resulting from the successful implementation of all net zero targets (as of December 2021) are 2.0°C (66%) and 2.7°C (90%)[3] above the pre-industrial baseline (Fig. 4, UNEP 2021a). Error ranges for the 66% and 90% likelihood estimates are provided in footnote #3 below.

3.2. Threats to Indo-Pacific Reef-building Corals

As described in the introductory paragraphs to this General Threats Evaluation and summarized in Table 2 above, the SRR (Brainard et al., 2011) and the 2014 final listing rule (79 FR 53851) define and rate the most important threats to the world's reef-building corals, based on information available at that time. In contrast, this Threats Evaluation is limited to Indo-Pacific reef-building corals, based on currently available information, leading to some slight changes in how threats are defined and rated. As explained in the following sub-sections, the most important threats to the Indo-Pacific corals based on currently available information are ocean warming (Factor E, Very High importance), ocean acidification (Factor E, High importance), disease (Factor C, High importance), fishing (Factor A, Medium importance), land-based sources of pollution (Factors A and E, Low-Medium importance), predation (Factor C, Low-Medium importance), collection and trade (Factor B, Low-Medium importance), sea-level rise (Factor E, Low importance), and the inadequacy of existing regulatory mechanisms (Factor D, High importance).

The effects of these threats are summarized from the SRR (Brainard et al. 2011) and final rule (79 FR 53851) as appropriate for the Indo-Pacific, as well as the substantial amount of new, relevant information that has become available since 2014. Conclusions are provided for each threat in terms of changes since 2014, projections for the foreseeable future, and the relative importance rating of each threat based on current information.

In order to summarize new information on observed and projected climate change-related threats (ocean warming, ocean acidification, and sea-level rise) that has become available since the SRR (Brainard et al. 2011) and final rule (79 FR 53851) were published, we use information from the Intergovernmental Panel on Climate Change's (IPCC) Sixth Assessment Report (AR6) and other published scientific literature. AR6 (IPCC 2021) describes historical global climate change, including observed ocean warming, ocean acidification, and sea-level rise. AR6 also projects ocean warming, ocean acidification, and sea-level rise over the remainder of the 21st century using a set of nine Shared Socio-economic Pathways (SSPs) that provide a standard framework for consistently

---

means there is a 90% chance that warming will be kept to 3.4°C or lower, and a 10% chance that warming will exceed 3.4°C, under current policies by 2100.

[2] Likelihood estimates of global warming above the pre-industrial baseline by 2100 assuming continuation of current policies, as of December 2021 (UNEP 2021a, p. 36):

- 66%: 2.6°C (range = 2.1–3.0°C). I.e., there is a 66% chance that warming will be kept to 2.6°C or lower.
- 90%: 3.4°C (range = 2.8–3.9°C). I.e., there is a 90% chance that warming will be kept to 3.4°C or lower.

[3] Likelihood estimates of global warming above the pre-industrial baseline by 2100 assuming successful implementation of all net zero policies, as of December 2021 (UNEP 2021a, p. 36):

- 66%: 2.0°C (range = 1.8–2.3°C). I.e., there is a 66% chance that warming will be kept to 2.0°C or lower.
- 90%: 2.7°C (range = 2.3–3.1°C). I.e., there is a 90% chance that warming will be kept to 2.7°C or lower.

modeling future climate change under different assumptions, including a core set of five scenarios that are the focus of AR6. These five scenarios span a wide range of plausible societal and climatic futures from potentially below 1.5°C best-estimate warming to over 4°C warming by 2100 (IPCC 2021, Figure 1.25). AR6's SSP scenarios incorporate the Representative Concentration Pathway (RCP) scenarios from the IPCC's Fifth Assessment Report (AR5, IPCC 2013), thus the SSPs are named after the RCP scenario that they are most similar to. For example, SSP2-4.5 is most similar to RCP4.5 from AR5 (IPCC 2021).

As described in Section 2.1 above, the effects of current GHG management policies are projected to result in 2.6–3.4°C of global warming above the pre-industrial baseline by 2100 (Fig. 4). Thus, projections of ocean warming over the foreseeable future (now to 2100) in the Indo-Pacific provided in the following section are based on the assumption that this level of global warming will occur between now and 2100, which is roughly equivalent to the AR6's combined projections for SSP2-4.5 and SSP3-7.0. Projections of ocean acidification and sea-level rise over the foreseeable future in the Indo-Pacific provided in the following sections are also based on AR6's combined projections for SSP2-4.5 and SSP3-7.0 (IPCC 2021). AR6's Interactive Atlas provides projections of climate variables over different 21st century timeframes under the SSP scenarios for all parts of the world compared to various historical baselines. The following projections of sea surface temperature (SST), surface pH, and sea-level rise are summarized from the Atlas for the foreseeable future (i.e., from the present to 2100) under the SSP2-4.5 and SSP3-7.0 scenarios for the Indo-Pacific in terms of change from the pre-industrial baseline of 1850-1900.

3.2.1. Ocean Warming (Factor E)

Ocean warming refers to the ongoing warming of the world's oceans from anthropogenic global climate change, causing warming-induced bleaching and mortality of corals. Because of the sharp increase in warming-induced coral bleaching and mortality since the 1980s, ocean warming was rated as "High" in terms of its relative importance to the extinction risk of the world's reef-building corals in the 2014 final listing rule (79 FR 53851), as shown in the left columns of Table 2 above. Ocean warming was considered the most important threat in the decision to list 20 of those species including the 15 Indo-Pacific species (79 FR 53851). Ocean warming is summarized here based on the SRR and the final rule, as well as new information that has become available since then, in terms of: (1) observed ocean warming to date within the Indo-Pacific, including trends since the 2014 listings; (2) projected ocean warming within the Indo-Pacific in the foreseeable future (i.e., from now to 2100); (3) observed effects of warming-induced mass bleaching on Indo-Pacific reef coral communities to date, including trends since the 2014 listings; and (4) projected effects of warming-induced mass bleaching on Indo-Pacific reef coral communities in the foreseeable future.

Observed Ocean Warming. The oceans influence climate by storing and transporting large amounts of heat, freshwater, and carbon. The ability of the oceans to store vast amounts of heat reflects the large mass and heat capacity of seawater relative to air. The oceans absorb most of the excess heat produced by greenhouse gas warming, resulting in warmer oceans and changes in global climate feedback loops. Heat absorption directly impacts the chemical and physical properties of the ocean, while moderating the effects of GHG emissions on land. Heat is absorbed first in the ocean's upper layers but eventually penetrates to all depths. Heat that is not absorbed by the ocean will warm the land, causing land and sea ice to melt (IPCC 2013, 2018, 2021).

Global mean SSTs increased by 0.88°C from the pre-industrial baseline period of 1850–1900 to 2011–2018, with 0.60°C of this warming having occurred since 1980. The tropical oceans have been warming faster than other regions since 1950, with the fastest warming in the equatorial Indian Ocean and the Coral Triangle area of the western Pacific Ocean. In contrast, the eastern Pacific Ocean has warmed more slowly than the global average (IPCC 2021, Figure 9.3, Table 2.4).

AR6 was based on data collected through 2018, but data collected by the NOAA National Centers for Environmental Information (NCEI) since then show a continued increase in global mean SSTs as well as those within the Indo-Pacific from 2019 to 2022 (NCEI 2022). The recent continuation of ocean warming has led to a sharp increase in anomalous warm seawater events known as "marine heatwaves" in the Indo-Pacific and elsewhere (Eakin et al. 2019, Oliver et al. 2021).

Projected Ocean Warming. Projections of global mean SSTs from now to 2100 under SSP1-2.6, SSP2-4.5, SSP3-7.0, and SSP5-8.5 are shown in Figure 9.3 of AR6 (IPCC 2021) compared to the 1950-1980 baseline when SSTs had already risen a few tenths of a degree Celsius above the pre-industrial baseline. Under SSP2-4.5, global mean SSTs are projected to increase approximately 2°C above the 1950-1980 baseline by 2100, or slightly more than 2°C above the pre-industrial baseline by 2100. Under SSP3-7.0, global mean SSTs are projected to increase slightly under 3°C above the 1950-1980 baseline by 2100, or approximately 3°C above the pre-industrial baseline by 2100. As shown in Figure 9.3 for SSP5-8.5, SST projections are spatially highly variable between and within the world's oceans, including within the Indo-Pacific.

Regional projections of increases in mean SSTs within the Indo-Pacific are provided by AR6's Interactive Atlas. For the long-term (2081-2100) under SSP2-4.5 within the approximately 20 IPCC reference regions that overlap with the ranges of the listed corals, mean SSTs in most regions are projected to increase by 2.0-2.5°C over the pre-industrial baseline, while some (e.g., Persian Gulf, Equatorial Pacific) are projected to increase by approximately 2.5°C or even more. For the long-term under SSP3-7.0 within these regions, mean SSTs in most regions are projected to increase by 2.75-3.25°C over the pre-industrial baseline, while some (e.g., Red Sea, Northeastern Africa) are projected to increase by over 3.5°C or even approximately 4.0°C (Persian Gulf).

Observed Effects of Warming-Induced Coral Bleaching. Elevated seawater temperatures lead to coral bleaching, the expulsion of the coral's symbiotic zooxanthellae in response to stress. Corals can withstand mild to moderate bleaching, but prolonged, severe, or repeated bleaching can lead to colony mortality. While coral bleaching patterns are complex, there is general agreement that thermal stress led to accelerated bleaching and mass mortality during the several decades preceding listing in 2014 (Brainard et al. 2011, 79 FR 53851). More recently, the coral bleachings across the Indo-Pacific, especially in 2014-2017, have been the longest, most widespread, and most damaging warming-induced coral bleaching events on record (Hughes et al. 2017a,b, Kayanne et al. 2017, Couch et al. 2017, Eakin et al. 2019, Lough et al. 2018, Skirving et al. 2019, Baumann et al. 2021). In addition, there were multiple widespread coral bleachings in parts of the Indo-Pacific between 2019 and 2022 (Cheung et al. 2021, Speare et al. 2022, Moriarty et al. 2023). Since 2014, the frequency, intensity, and magnitude of mass coral bleaching events in the Indo-Pacific have rapidly increased, marking the transition to a new era in which bleaching refugia are shrinking, and intervals between recurrent bleachings are too short for recovery (Hughes et al. 2018a,b, Dietzel et al. 2020, Dixon et al. 2022, Hughes et al. 2021).

The capacity of reef-building corals to acclimatize or adapt to changing environmental conditions such as warming seawater temperatures may buffer some species or populations from the full effects of warming-induced bleaching events (Brainard et al. 2011, Burt et al. 2020, Putnam 2021, Putnam et al. 2017). There are many documented examples of acclimatization or adaptation of Indo-Pacific corals to ocean warming (Brainard et al. 2011, Palumbi et al. 2014, Hughes et al. 2018c, Bairos-Novak et al. 2021, IPCC 2022, Elder et al. 2022, Smith et al. 2022). Although these examples demonstrate that the general acclimatization and adaptation capacity of Indo-Pacific reef-building corals has sometimes limited the impacts of ocean warming, they also show that any such capacity is highly dependent on species, location, habitat type, and many other factors.

Projected Effects of Warming-Induced Coral Bleaching. The responses of the world's corals and coral reef ecosystems to ocean warming and other threats in the 21st century under SSP2-4.5 and SSP3-7.0 are approximated by models of the most similar AR5 scenarios or global warming levels. Projections of the effects of ocean warming under RCP4.5 (similar to AR6's SSP2-4.5) include sharp increases in coral disease (Maynard et al. 2015), the onset of Annual Severe Bleaching on >75% of the world's coral reefs by mid-century (van Hooidonk et al. 2016), and the likely elimination of most coral reefs by 2040–2050 (Hoegh-Guldberg et al. 2017). A projection of the effects of ocean warming under an assumed global warming level of 3.0°C by 2100 (roughly equal to SSP3-7.0) concluded that the world's coral reefs would experience 23 times more thermal stress than all of the historical bleaching events combined from the late 1800s to 2016 (Lough et al. 2018). That is, the projected effects of warming-induced bleaching would be severe under either SSP2-4.5 or SSP3-7.0 (IPCC 2022).

As noted above, acclimatization and adaptation has been observed to sometimes limit the effects of ocean warming on reef-building corals. However, recent models incorporating physiological, ecological, and evolutionary processes find limited ability to adapt this century at rates of warming projected under RCP4.5 (similar to SSP2-4.5), RCP6.0 (slightly less warming than SSP3-7.0), and RCP8.5 (more warming than SSP3-7.0; Matz et al. 2020, McManus et al. 2020, Logan et al. 2021, IPCC 2022). For example, based on Logan et al. (2021), IPCC (2022) projected conditions of the world's coral reefs under the four RCPs assuming "no adaptation" vs. "with adaptation" by 2100. With no adaptation, over 90% of all coral reefs would be eliminated by 2100 under either RCP4.5 or RCP6.0, and those that remained would be degraded. With adaptation, approximately 30% and 80% of all coral reefs would be eliminated by 2100 under RCP4.5 and RCP6.0, respectively, and those that remained would be either low diversity or degraded (IPCC 2022).

Ocean Warming Conclusion. Based on the above summaries and cited information, we conclude that: (1) ocean warming and warming-induced coral bleaching has substantially worsened since the 15 corals were listed in 2014, as illustrated by the series of marine heatwaves and subsequent mass coral bleaching events across the Indo-Pacific from 2014 to 2017, the most severe and widespread on record, as well as multiple events since 2019; and (2) ocean warming and coral bleaching are projected to greatly worsen in the foreseeable future under SSP2-4.5 and SSP3-7.0, even assuming broad coral adaptation capacity. Since ocean warming has substantially worsened since 2014, current projections indicate that this threat is likely to greatly worsen in the foreseeable future, and current information suggests that the capacity of Indo-Pacific corals to adapt to ocean warming is limited, we rate the current importance of ocean warming to the extinction risk of Indo-Pacific reef-building corals as "Very High," as shown in the right columns of Table 2 above (up from "High" in the 2014 final rule for the world's reef-building corals). We consider ocean warming to be the most important threat to the 15 listed corals and Indo-Pacific coral reef ecosystems in general.

3.2.2. Ocean Acidification (Factor E)

Ocean acidification refers to the ongoing decrease in pH of the world's oceans, as they continue to absorb the increasing CO_2 in the atmosphere. Ocean acidification reduces coral calcification and erodes the physical structure of coral reefs, and was rated as "Medium-High" in terms of its relative importance to the extinction risk of the world's reef-building corals in the 2014 final listing rule (79 FR 53851), as shown in the left columns of Table 2 above. Ocean acidification is summarized here based on the SRR (Brainard et al. 2011), the 2014 final listing rule (79 FR 53851), and new information that has become available since then, in terms of: (1) observed ocean acidification to date within the Indo-Pacific; (2) projected ocean acidification within the Indo-Pacific in the foreseeable future (i.e., from now to 2100); (3) observed effects of ocean acidification on Indo-Pacific reef coral communities to date; and (4) projected effects of ocean acidification on Indo-Pacific reef coral communities in the foreseeable future.

Observed Ocean Acidification. The rising atmospheric CO_2 concentrations and corresponding increase in CO_2 uptake by the oceans has led to a reduction in global mean surface pH in the open ocean of slightly more than 0.1 pH units from approximately 8.2 to <8.1 units since the pre-industrial baseline period of 1850 to 1900. Between 1985 and 2020 in the low-latitudes (i.e., 30°N–30°S, an area that includes most of the Indo-Pacific's coral reefs), mean surface pH in the open ocean dropped from approximately 8.10 to 8.06. Mean surface pH in the open ocean varies spatially by seawater temperature, upwelling, and other factors. Within the Indo-Pacific, areas with lowest surface pH are mostly those with strong upwelling, such as along the east Africa coast and within the eastern equatorial Pacific (IPCC 2021).

Ocean acidification reduces the aragonite saturation state (Ω_{arg}) in seawater by lowering the supersaturation of carbonate minerals including aragonite, which requires marine calcifiers like reef-building corals to expend more energy to calcify their skeletons. Mean Ω_{arg} of the surface waters of the open ocean across the tropical Indo-Pacific decreased from approximately 4.0-4.5 in the pre-industrial era to 3.5-4.0 in recent decades (Feely et al. 2009, 2012, Ishii et al. 2020). As of 2012, mean annual Ω_{arg} of the surface waters of the open ocean in the tropical Indo-Pacific ranged from approximately 3.2 (eastern equatorial Pacific) to 4.0 (central south Pacific), with the western Pacific and Indian Oceans at intermediate levels (Jiang et al. 2015). Since then, the rate of ocean acidification and associated Ω_{arg} declines in the surface waters of the open ocean have accelerated in the Pacific (Ono et al. 2019, Ishii et al. 2020) and Indian Oceans (Panchang and Ambokar 2021).

Projected Ocean Acidification. Under SSP2-4.5 and SSP3-7.0, global mean surface pH of the open ocean is projected to decrease from approximately 8.1 in 2020, to 7.9 and 7.8 by 2100, respectively (IPCC 2021, Fig. 4.8). Regional projections of decreases in mean pH within the Indo-Pacific are provided by AR6's Interactive Atlas. For the long-term (2081-2100) under SSP2-4.5 within the approximately 20 IPCC reference regions that overlap with the ranges of the listed corals, mean surface pH of the open ocean is projected to decrease by 0.15 to 0.20 pH units from current levels. For the long-term under SSP3-7.0 within these regions, mean surface pH of the open ocean is projected to decrease by 0.20 to 0.30 pH units from current levels (IPCC 2021).

AR6 (IPCC 2021) does not include Ω_{arg} projections for the SSPs, as of August 2022. Matear et al. (2018) projected Ω_{arg} under AR5's RCP4.5, a similar scenario to AR6's SSP2-4.5, finding that Ω_{arg} would decrease to <3.0 across approximately half to three-quarters of the surface waters of the open ocean within the Indo-Pacific by 2090. Hoegh-Guldberg et al. (2017) modeled Ω_{arg} at an atmospheric CO_2 level of 800 ppm (roughly equivalent to SSP3-7.0 in 2100), finding that Ω_{arg} would decrease to <3.0 in nearly all of the surface waters of the open ocean within the Indo-Pacific.

Observed Effects of Ocean Acidification. Ocean acidification affects reef-building corals primarily through decreased calcification of coral colonies (leading to lower skeletal growth rates) and increased dissolution of the calcium carbonate structure of coral reefs (leading to reef erosion rates outpacing accretion rates), although there are other impacts as well, such as on coral reproduction (leading to lower fertilization, settlement, and recruitment; Brainard et al. 2011, 79 FR 53851). Many studies report decreases in calcification and skeletal growth rates of reef-building corals across the Indo-Pacific in recent decades, with ocean acidification and ocean warming considered the most important factors (e.g., Mollica et al. 2018, Steiner et al. 2018, Kang et al. 2021).

Guo et al. (2020) devised a coral growth model to isolate the impacts of ocean acidification on skeletal growth of massive *Porites* colonies from ocean warming and other factors, finding that ocean acidification alone reduced skeletal growth by 13 ± 3% on the GBR since 1950. Other studies indicate that ocean acidification has resulted in reductions in ecosystem-scale coral reef calcification (i.e., corals and crustose coralline algae) in the Indo-Pacific (Smith et al. 2020, Davis et al. 2021). Increases in erosion rates of Indo-Pacific coral reefs are also occurring, most likely because ocean acidification is exacerbating the impacts of more frequent and severe warming-induced bleaching events, storms, and other disturbances (Eyre et al. 2018, Steiner et al. 2018, Torda et al. 2018).

Projected Effects of Ocean Acidification. Projections of the effects of ocean acidification under scenarios or global warming levels similar to SSP2-4.5 and SSP3-7.0 include sharp decreases in coral calcification (Hoegh-Guldberg et al. 2017, Albright et al. 2018, Kornder et al. 2018, IPCC 2018), increased reef erosion and dissolution of reef substrates (Cornwall et al. 2021, Davis et al. 2021, IPCC 2022), and impacts to coral reproduction such as reduced settlement (Fabricius et al. 2017, IPCC 2022). The projected impacts of ocean acidification have severe implications for reef-building corals, even if they were occurring in the absence of other threats. But they will be occurring simultaneously with the effects of ocean warming and other threats, thereby exacerbating their impacts (Hough-Guldberg et al. 2017, Klein et al. 2021). The combined effects of projected ocean acidification and ocean warming are expected to result in reductions in coral reef complexity and resilience, decreasing populations of reef-building corals especially sensitive species, increases in macroalgae, and overall habitat simplification and degradation (Agostini et al. 2018, IPCC 2018, 2022).

Ocean Acidification Conclusion. Based on the above summaries and cited information, we conclude that: (1) ocean acidification and its effects on Indo-Pacific reef-building corals and coral reefs have been occurring for decades, and have worsened since the 15 corals were listed in 2014, as shown by decreased coral and crustose coralline algae calcification rates and increased reef erosion rates; and (2) ocean acidification and its effects on Indo-Pacific reef-building corals and coral reefs are projected to greatly worsen in the foreseeable future under SSP2-4.5 and SSP3-7.0, especially in terms of interactions with other threats. Since ocean acidification has substantially worsened since 2014, current projections indicate that this threat is likely to greatly worsen in the foreseeable future, and current information suggests that the capacity of Indo-Pacific corals to adapt to ocean acidification is limited, we rate the current importance of ocean acidification to the extinction risk of Indo-Pacific reef-building corals as “High” (up from “Medium-High” in the 2014 final rule for the world’s reef-building corals), as shown in the right columns of Table 2 above.

3.2.3. Disease (Factor C)

Disease refers to infectious diseases of reef-building corals, which adversely affect various coral life history stages by causing adult mortality, reducing reproductive success, and impairing colony growth. Because disease commonly results from a combination of local stressors and climate change that are projected to greatly increase in the foreseeable future, disease was rated as “High” in terms of its relative importance to the extinction risk of the world’s reef-building corals in the 2014 final listing rule (79 FR 53851), as shown in the left columns of Table 2 above. Disease is summarized here based on the SRR (Brainard et al. 2011), the final rule, and new information that has become available since then, in terms of: (1) observed effects of disease on Indo-Pacific reef-building corals to date; and (2) projected effects of disease on Indo-Pacific reef-building corals in the foreseeable future.

Observed Effects of Disease. Most information on disease is from the Caribbean, where it is more common and better documented. Region-wide patterns of the prevalence of disease in the Indo-Pacific are relatively difficult to determine because of the high diversity of both reef-building coral species and their diseases, the vast size of the region, and the lack of data across the appropriate spatial and temporal scales. Some of the most common diseases are white syndrome, black band disease, brown band disease, skeletal eroding band and growth anomalies, all of which have been documented at numerous locations around the Indo-Pacific. Disease in the Indo-Pacific may have increased over the last few decades, but trend data are lacking. What is certain is that the stressors associated with disease, such as elevated seawater temperatures, sedimentation, and excessive nutrients, have rapidly increased during this period in the Indo-Pacific (Brainard et al. 2011, 79 FR 53851).

Since the 15 corals were listed in 2014, disease has been increasingly reported from across the Indo-Pacific (e.g., Bourne et al. 2015, Thangaradjou et al 2016, Rodríguez-Villalobos and Reyes-Bonilla 2019, Greene et al. 2020, Howells et al. 2020). Globally, disease distributions are both diverse and widespread across all ocean basins, indicating hotspots in both the Indo-Pacific and the Caribbean (Vega Thurber et al. 2020). Since 2014, the stressors associated with disease have increased rapidly in the Indo-Pacific, especially the warming events and subsequent coral bleaching and mortality in 2014–2017. Disease outbreaks associated with these warming events have occurred in many locations within the Indo-Pacific (e.g., Hadaidi et al. 2018, Kubomura et al. 2018, Brodnicke et al. 2019, Aeby et al. 2020). Disease outbreaks are also associated with LBSP (e.g., Oberle et al. 2019), and the interactive effects of ocean warming and LBSP are also contributing to more widespread disease in the Indo-Pacific (MacNeil et al. 2019, Vega Thurber et al. 2020).

Projected Effects of Disease. The projected effects of disease in the foreseeable future on Indo-Pacific coral reefs under SSP2-4.5 and SSP3-7.0 are likely to substantially increase, given that disease outbreaks typically are caused by other threats, especially ocean warming and LBSP, both of which are projected to increase in the foreseeable future under both scenarios. The following papers model projected disease under various scenarios to 2100: (1) Maynard et al. (2015) projected that disease under RCP8.5 (somewhat worse than SSP3-7.0) would sharply increase globally including in the Indo-Pacific over the 21st century, and that disease would cause as much coral mortality as bleaching in the coming decades; (2) Zvuloni et al. (2015) projected that white plague disease in Red Sea corals under additional warming of 0.5°C and 1.0°C (less than either SSP2-4.5 or SSP3-7.0) would result in sharply increased epidemics under either scenario over the 21st century; and (3) Burke et al. (2023) projected that 76.8% of the world's reef-building corals would be diseased by 2100 under the equivalent of RCP8.5 (somewhat worse than SSP3-7.0).

Disease Conclusion. Based on the above summaries and cited information, we conclude that: (1) the effects of disease on Indo-Pacific corals have increased since the 15 corals were listed in 2014, mainly in response to the 2014 – 2017 bleaching events; (2) these effects are likely to substantially increase in the foreseeable future under SSP2-4.5 and SSP3-7.0; and (3) the current importance of disease to the extinction risk of Indo-Pacific reef-building corals is "High," as shown in the right columns of Table 2 above.

3.2.4. Fishing (Factor A)

The SRR (Brainard et al. 2011) and 2014 final listing rule (79 FR 53851) treated the "Direct Habitat Impacts" (i.e., direct effects) and "Trophic Effects" (i.e., indirect effects) of fishing on the world's reef-building corals as separate threats. The direct effects of fishing refer to the habitat impacts of fishing gear and practices, while indirect threats refer to ecological impacts of removing certain types of fish from coral reefs, otherwise known as the trophic effects of fishing. The direct and indirect effects of fishing were rated as "Low" and "Medium" importance to the world's reef-building corals in the final rule, respectively, the latter of which is shown in the left columns of Table 2 above. As a result of treating the direct effects of fishing as a separate threat and its low rating, it was not included in the list of the most important threats to corals in the final listing rule (79 FR 53851).

The direct and indirect effects of fishing on reef-building corals may not be readily distinguishable from one another, especially when several other threats are also present, which is almost always the case. For example, direct and indirect effects of fishing both lead to reduction in reef fish biomass, simplification of reef structure, and increases in macroalgae. Given that: (1) the purpose of the threats evaluation is to provide information that is needed to determine the status of the 15 listed corals and to formulate actions needed to recover the species; and (2) fine distinctions between threats are not useful for determining status, and recovery actions to address the direct and indirect effects of fishing are likely to be very similar if not identical, this RSR combines the direct and indirect effects of fishing into a single threat.

Fishing refers to the harvest of finfish, mollusks, crustaceans, and other forms of marine animal and plant life on or in the vicinity of shallow coral reefs and reef-building corals, either for food or for the aquarium trade. Harvest of corals themselves is treated separately under Collection and Trade below. Fishing is summarized here based on the SRR (Brainard et al. 2011), the 2014 final listing rule (79 FR 53851), and new information that has become available since then, in terms of: (1) observed effects of fishing on Indo-Pacific reef-building corals to date; and (2) projected effects of fishing on Indo-Pacific reef-building corals in the foreseeable future (i.e., from now to 2100).

Observed Effects of Fishing. Fishing directly affects the habitats of reef-building corals and the coral colonies themselves when various gears or fishing methods come into contact with reef substrates. Gillnets and traps damage corals and other sessile fauna via movement during even mild storm events and during gear retrieval in adverse conditions. Lost or abandoned fishing gear (derelict gear) becomes entangled on coral reefs, continuing to damage corals through abrasion for months or years. Fishers in some parts of the world employ destructive methods such as blasting or poisoning to harvest fish and invertebrates from coral reefs, killing or damaging corals. Direct fishing impacts on corals are particularly high in heavily-populated parts of the Indo-Pacific with high densities of poorly-regulated coral reef fisheries, such as Southeast Asia, eastern Africa, and others (Brainard et al. 2011, 79 FR 53851).

Since the 15 corals were listed in 2014, the direct effects of fishing on corals and coral reefs have continued across much of the Indo-Pacific (e.g., Ballesteros et al 2018, Mbaru et al 2019, Figueroa-Pico et al 2020). Although blast fishing is illegal in nearly all countries in the Indo-Pacific (NMFS 2012, Dunning 2014), it persists in some places (Slade and Kalangahe 2015, Veloria et al 2021). The direct effects of legal fishing on coral reefs are very widespread and growing as the human population grows, especially in the Coral Triangle area and east Africa (Riegl and Glynn 2020). Other factors may be reducing direct effects in certain areas, including the ongoing shift of populations in many Indo-Pacific countries from rural to urban areas (UN-Habitat 2015), and the growth of no-take marine protected areas (Lewis et al. 2017, Williams et al. 2019, Campbell et al. 2020). However, the increasingly severe impacts of ocean warming, ocean acidification, and other threats are reducing the overall health of Indo-Pacific coral reefs, likely reducing their capacity to withstand the direct effects of fishing.

In addition to the direct effects of fishing described above, fishing can also have indirect effects by reducing the populations of certain types of fish on coral reefs, such as herbivorous and piscivorous fish species. Fewer herbivorous fish results in less grazing of algae, which in turn allows algae to outcompete corals for space. Fewer piscivorous fish results in less predation on corallivorous fish species such as butterflyfish and parrotfish, allowing their populations to grow, which in turn leads to more predation of corals, providing a competitive advantage to macroalgae. These types of indirect effects are collectively referred to as “trophic effects of fishing” because fishing alters food web dynamics on coral reefs, typically in ways that are harmful to corals. In the Indo-Pacific, while high diversity of herbivorous reef fish assemblages and large coral reef ecosystems provide some resilience to fishing, trophic effects have been documented for decades (Brainard et al. 2011, 79 FR 53851).

Since the 15 corals were listed in 2014, the indirect effects of fishing on corals and coral reefs have continued across the heavily-fished portions of the Indo-Pacific such as parts of east Africa and the

Coral Triangle, as shown by studies comparing trophic structures of heavily vs. lightly-fished coral reefs (Graham et al. 2017, Ruppert et al. 2018, Heenan et al 2019, Robinson et al. 2020). The increasing number of marine protected areas that restrict or ban fishing has reduced indirect effects of fishing on Indo-Pacific coral reefs such as in some cases on the GBR and in the Red Sea and Fiji (Williams et al. 2016, 2019, Cinner et al. 2020), but not in others such as in some cases in the Philippines (Aurellado et al 2021). Similar to the direct effects of fishing, a larger problem is that the increasingly severe impacts of the other threats are likely reducing the capacity of Indo-Pacific coral reefs to withstand the indirect effects of fishing.

Projected Effects of Fishing. The effects of fishing on Indo-Pacific reef-building corals from now to 2100 depend on human populations throughout the region (Brainard et al. 2011, Riegl and Glynn 2020), many of which are expected to grow at higher rates than the mean global human population. For example, the countries in the Coral Triangle (Malaysia, Indonesia, Philippines, Papua New Guinea, Solomon Islands), where much of the coral reef area (Spalding 2001) and reef-building coral biodiversity (Veron et al. 2015) of the Indo-Pacific are located, all have projected population growth rates that exceed the global mean. Human populations are also expected to grow more rapidly in east Africa than the global mean (United Nations Population Division, https://population.un.org/wpp/, accessed Aug-22). Another factor that affects fishing pressure is fishing technologies (fishing gear, boats, etc.), which affect the capacity of the fisheries to find and catch fish even from distant and deep coral reefs. Generally, fishing technologies are rapidly advancing in much of the Indo-Pacific, and the rate of advancement is expected to increase in the foreseeable future (Silapajarn et al. 2017).

The projected direct and indirect effects of fishing in the foreseeable future on Indo-Pacific coral reefs under SSP2-4.5 and SSP3-7.0 are likely to substantially increase, given the following factors: (1) increasing human populations, especially in the Coral Triangle and east Africa; (2) advancement of fishing technologies; and (3) exacerbation of fishing effects by severe ocean warming and ocean acidification under both scenarios. Better fisheries management and more extensive marine protected areas have the potential to somewhat limit the effects of fishing, but it is not possible to project the degree to which they will be implemented in the foreseeable future.

Fishing Conclusion. Based on the above summaries and cited information, we conclude that: (1) the direct and indirect effects of fishing on Indo-Pacific corals have continued since the 15 corals were listed in 2014, likely intensifying in some locations while lessening in others due to various factors; and (2) these effects are likely to substantially increase in the foreseeable future under SSP2-4.5 and SSP3-7.0. As noted at the beginning of this section, the SRR and final rule treated the direct and indirect effects of fishing separately, rating their importance to the world's reef-building corals as "Low" and "Medium," respectively. This RSR combines direct and indirect effects into a single threat. Since the direct effects of fishing are more pronounced in the Indo-Pacific than in the Atlantic, we rate the importance of the combined direct and indirect effects of fishing on Indo-Pacific reef-building corals as "Medium," as shown in the right columns of Table 2 above.

3.2.5. Land-based Sources of Pollution (Factors A and E)

The SRR (Brainard et al. 2011) and 2014 final listing rule (79 FR 53851) treated the effects of sedimentation and nutrients originating from land on the world's reef-building corals as separate threats, both of which were rated as "Low-Medium" importance to the world's reef-building corals in the final rule, as shown in the left columns of Table 2 above. The effects of sedimentation and nutrients on reef-building corals may not be readily distinguishable from one another, especially when several other threats are also present, which is almost always the case. For example, sedimentation and nutrients both lead to lower coral growth, reduced coral reproductive output, and increases in macroalgae. Given that: (1) the purpose of the threats evaluation is to provide information that is needed to determine the status of the 15 listed corals and to formulate actions needed to recover the species; and (2) fine distinctions between threats are not useful for determining status, and recovery actions to address sedimentation and nutrients are likely to be very similar if not identical, this RSR combines the sedimentation and nutrients into land-based sources of pollution.

Land-based sources of pollution (LBSP) refers to sediment, nutrients, contaminants, salinity, and other types of pollution affecting reef-building corals that originate from agriculture, urbanization, logging, mining, road-building and other development in coastal and inland watersheds that make their way to the ocean by river discharge, groundwater seeps, and surface runoff. Because of the relatively high impacts of sediment and nutrients on reef-building corals compared to contaminants and salinity, LBSP here only includes sedimentation and nutrients. LBSP is summarized here based on the SRR (Brainard et al. 2011), the final rule (79 FR 53851), and new information that has become available since then, in terms of: (1) observed effects of LBSP on Indo-Pacific reef-building corals to date; and (2) projected effects of LBSP on Indo-Pacific reef-building corals in the foreseeable future (i.e., from now to 2100).

Observed Effects of LBSP. When terrestrial sediment enters the marine environment, it is deposited on substrates or suspended in the water column. The resulting sedimentation and turbidity impacts reef-building corals in several ways, including: (1) partial or complete colony mortality from smothering by sediment; (2) lower colony growth and reproductive output as energy is diverted to sediment displacement; (3) prevention or reduction of settlement and recruitment by sedimentation of substrates; and (4) blocking of light by turbidity, making less energy available for photosynthesis and growth. Land-clearing for agriculture and livestock grazing rapidly grew in many parts of the Indo-Pacific starting in the late 19th century, leading to sharp increases in sedimentation on coral reefs. In recent decades, the trend has worsened with the expansion of agriculture together with urbanization, logging, and mining. Overall, sedimentation is considered to be a primary cause of coral reef degradation and loss in many locations throughout the Indo-Pacific, including parts of the GBR and the Coral Triangle (Brainard et al. 2011, 79 FR 53851).

Many of the same human activities that result in sedimentation of coral reefs, especially agriculture and urbanization, also produce excessive nutrients (e.g., nitrogen and phosphorus in fertilizers, wastewater). These nutrients make their way to coral reefs via point and non-point sources such as river discharges, groundwater, and municipal outfalls. Excessive nutrients impact reef-building corals through reduced reproductive capacity and compromised skeletal growth, and indirectly by allowing higher growth of algae that compete with coral for space and stimulating plankton growth in the water column that increases turbidity. As with sedimentation, the proportion of coral reefs impacted by excessive nutrients has rapidly increased in recent decades, and nutrients are also considered to be a primary cause of coral reef degradation and loss in many locations throughout the Indo-Pacific. LBSP can also include contaminants, such as heavy metals, pesticides, antifoulants, and many others, resulting in localized impacts to corals (Brainard et al. 2011, 79 FR 53851).

Since the 15 corals were listed in 2014, deforestation, urbanization and industrialization have continued if not accelerated in many coastal watersheds of the Indo-Pacific, including within much of the Coral Triangle, throughout south Asia and east Africa, and in many Pacific Islands (e.g., Adyasari et al. 2021, Crompton et al. 2021, Zhang and Su 2022). The increasing development has likely exacerbated LBSP on adjacent coral reefs across much of the Indo-Pacific, as has been documented in many locations (Browne et al. 2019, Carlson et al. 2019, Guo et al. 2019, Adam et al. 2021). The weakening of corals by sediment and nutrients reduces their capacity to survive warming-induced bleaching and ocean acidification (Prouty et al. 2017, Allgeier et al. 2019, Tuttle and Donahue 2022), and compromises their recovery (MacNeil et al. 2019, IPCC 2022).

Projected Effects of LBSP. The projected effects of LBSP in the foreseeable future on Indo-Pacific coral reefs under SSP2-4.5 and SSP3-7.0 are likely to substantially increase, given the following factors: (1) increasing human populations, especially in the Coral Triangle and east Africa (United Nations Population Division, https://population.un.org/wpp/); (2) the most rapid industrialization in the world through 2050 is projected to be in south and southeastern Asia (PwC 2017); and (3) exacerbation of LBSP impacts by severe ocean warming and ocean acidification under both scenarios (IPCC 2022). While the impacts of LBSP on corals and coral reefs will likely continue growing in many locations around the Indo-Pacific, an increasing number of coastal areas and watersheds adjacent to coral reefs are being included in new protected areas throughout the Indo-Pacific (UNEP 2021b) or actively managed to reduce LBSP at the watershed scale (Richmond et al. 2019), potentially controlling or reducing the impacts of LBSP on coral reefs in some locations. However, while more extensive coastal protected areas and better watershed management have the potential to somewhat limit the impacts of LBSP (Richmond et al. 2019, UNEP 2021b), it is not possible to project the degree to which they will be implemented in the foreseeable future.

LBSP Conclusion. Based on the above summaries and cited information, we conclude that: (1) the effects of LBSP on Indo-Pacific corals have continued since the 15 corals were listed in 2014, likely intensifying in some locations while lessening in others due to various factors; (2) these effects are likely to substantially increase in the foreseeable future under SSP2-4.5 and SSP3-7.0; and (3)the current importance of LBSP to the extinction risk of Indo-Pacific reef-building corals is "Medium-High," as shown in the right columns of Table 2 above.

3.2.6. Predation (Factor C)

Predation refers to feeding upon reef-building corals by corallivorous species of invertebrates and fish. Outbreaks of the crown-of-thorns seastar (COTS) are among the most significant disturbances affecting Indo-Pacific reef-building corals. The importance of predation to the extinction risk of the world's reef-building corals was rated as "Low" in the 2014 final listing rule (79 FR 53851), as shown in the left columns of Table 2 above. However, predation was still considered one of the most important threats in the decision to list the 15 corals (79 FR 53851). Predation is summarized here based on the SRR and the final rule, and new information that has become available since then, in terms of: (1) observed effects of predation on Indo-Pacific reef-building corals to date; and (2) projected effects of predation on Indo-Pacific reef-building corals in the foreseeable future.

Observed Effects of Predation. Predation on some Indo-Pacific reef-building coral genera, especially *Acropora, Montipora, Pocillopora*, and *Porites*, by COTS, *Drupella* snails, fish, and other corallivores is a chronic energy drain. Predator outbreaks, especially by COTS, can result in major disturbances by wiping out coral cover over a large area in a short period of time. COTS outbreaks in some areas are thought to be caused by LBSP that results in phytoplankton blooms which, in turn, provide food for COTS larvae, allowing their populations to grow quickly. COTS outbreaks may be facilitated by removal of their predators such as large sea snails and reef fish through collection and fishing, as well as through the trophic effects of fishing which allow algae to outcompete and weaken corals thereby making them more susceptible to predation (Brainard et al. 2011, 79 FR 53851).

Since the 15 corals were listed in 2014, COTS outbreaks remain one of the most significant disturbances and major causes of coral loss across the Indo-Pacific (Pratchett et al. 2017, Plaganyi et al 2020), while outbreaks of other predators such as *Drupella* are also important locally (Koido et al 2017, Bessey et al. 2018). The bleaching events of 2014–2017 resulted in increased predation on corals in some locations (Vanhatalo et al 2016, Keesing et al. 2019, Tkachenko and Huang 2022), as did disease (Nicolet et al. 2018, Renzi et al. 2022). These impacts have likely been further exacerbated by the additional bleaching events that have occurred since 2017 (see Ocean Warming section above). COTS (Haywood et al 2019, Vercelloni et al. 2017) and *Drupella* (Bruckner et al.

2017) outbreaks have been shown to reduce coral resilience and inhibit recovery from bleaching events.

Projected Effects of Predation. The projected effects of predation in the foreseeable future on Indo-Pacific coral reefs under SSP2-4.5 and SSP3-7.0 are likely to substantially increase, because: (1) as described above, ocean warming, ocean acidification, fishing, land-based sources of pollution, and disease all are projected to increase under both scenarios in the foreseeable future, all of which make corals more susceptible to predation; and (2) COTS larvae grow faster under the levels of ocean warming and ocean acidification projected for these scenarios than under current conditions (Kamya et al. 2017, 2018).

Predation Conclusion. Based on the above summaries and cited information, we conclude that: (1) the effects of predation on Indo-Pacific corals have increased since the 15 corals were listed in 2014, mainly because the 2014 – 2017 bleaching events resulted in more favorable conditions for predators such as COTS, as well as multiple events since 2019; and (2) the effects of predation are likely to substantially increase in the foreseeable future under SSP2-4.5 and SSP3-7.0. Since factors that exacerbate predation have increased since 2014, especially ocean warming, and current projections indicate that these factors are likely to greatly worsen in the foreseeable future, we rate the current importance of predation to the extinction risk of Indo-Pacific reef-building corals as "Low-Medium," as shown in the right columns of Table 2 above (up from "Low" in the 2014 final rule for the world's reef-building corals).

3.2.7. Collection and Trade (Factor B)

Collection and trade refers to the process of taking reef-building corals from their natural habitat (collection) to supply the international and domestic marine aquarium, ornamental and curio industries (trade). Coral populations are impacted directly by removal of individual colonies, and indirectly by altering or destroying coral habitat during the collection process. The collection and trade industry has grown substantially over the last several decades. The importance of collection and trade to the extinction risk of the world's reef-building corals was rated as "Low" in the 2014 final listing rule (79 FR 53851), as shown in the left columns of Table 2 above. However, collection and trade was still considered one of the most important threats in the decision to list the 15 corals (79 FR 53851). Collection and trade is summarized here based on the SRR (Brainard et al. 2011), the 2014 final listing rule (79 FR 53851), and new information that has become available since then, in terms of: (1) observed effects of collection and trade on Indo-Pacific reef-building corals to date; and (2) projected effects of collection and trade on Indo-Pacific reef-building corals in the foreseeable future.

Observed Effects of Collection and Trade. Millions of live coral colonies or fragments have been collected annually from Indo-Pacific coral reefs over the last several decades to supply marine aquarium demand, mainly from the United States, the European Union, and Japan. Nearly all reef-building corals are listed under Appendix II of the Convention on International Trade in Endangered Species' (CITES), which regulates and tracks international trade of these species to avoid utilization incompatible with their survival. The CITES collection and trade database (https://trade.cites.org) shows a steady increase in international trade since the 1980s, mostly from wild collection, although some production has shifted to captive culture (i.e., land-based and ocean-based artificial propagation). The ten most popular coral genera in the global marine aquarium trade have been *Acropora, Euphyllia, Goniopora, Trachyphyllia, Plerogyra, Montipora, Heliofungia, Lobophyllia, Porites*, and *Turbinaria*, all of which are Indo-Pacific reef-building corals. Collection of corals from their natural habitat is usually destructive to the reef habitat around the corals, and can result in removing and discarding large amounts of live coral that go unsold. While collection is typically focused on small parts of a coral reef, it can result in significant impacts to that reef and may contribute to individual species' extinction risk (Brainard et al. 2011, 79 FR 53851).

Since the 15 corals were listed in 2014, international collection and trade of marine species, including reef-building corals, has continued to grow at a rapid pace (Pavitt et al. 2021). According to the CITES database, international trade continued to grow for most listed coral genera including *Acropora* (NMFS 2022a). Although the CITES database is a valuable source of information on coral collection and trade, it likely does not represent the total amount of coral collection and trade that is occurring globally because: (1) not all countries submit their coral import/export reports to CITES, and many submit them years late (Pavitt et al. 2021); (2) it likely undercounts for several other reasons, such as taxa identification challenges, undocumented or illegal trade, etc. (CBD 2020, 2021); and (3) it only tracks international trade, but legal and illegal collection of corals for domestic curio markets occur in some countries (UNEP-WCMC 2015) and can result in major impacts on corals (e.g., Glynn 2001). However, there are other factors that have recently slowed the growth of wild collection of corals, including: (1) reduction due to the covid pandemic (Grand View Research 2022); (2) bans on wild collection in major exporting countries including Fiji (2017) and Indonesia (2018); and (3) the increasing prevalence of captive culture (NMFS 2022a).

<u>Projected Effects of Collection and Trade</u>. The projected effects of collection and trade in the foreseeable future on Indo-Pacific coral reefs under SSP2-4.5 and SSP3-7.0 are likely to substantially increase because: (1) the global demand for marine aquarium animals including corals is likely to increase (Pavitt et al. 2021); (2) population and economic growth are both projected to increase over at least the next several decades, resulting in more demand for luxury items such as marine aquarium species; and (3) the worsening of ocean warming and ocean acidification may compound the localized impacts of coral collection. The impacts of the projected growth of the marine aquarium industry on corals may be moderated somewhat by the simultaneous increase in captive culture.

<u>Collection and Trade Conclusion</u>. Based on the above summaries and cited information, we conclude that: (1) collection and trade has remained an important threat since the 15 corals were listed in 2014, but information is inadequate to determine overall trends; and (2) the effects of collection and trade are likely to substantially increase in the foreseeable future under SSP2-4.5 and SSP3-7.0. Since the factors that exacerbate the effects of collection and trade (i.e., increasing demand, population and economic growth, and worsening of threats that compound effects) are all expected to substantially increase in the foreseeable future, the effects of collection and trade on Indo-Pacific reef-building corals are likely to be higher than anticipated in 2014. Thus, we rate the current importance of collection and trade to the extinction risk of Indo-Pacific reef-building corals as "Low-Medium," as shown in the right columns of Table 2 above (up from "Low" in the 2014 final rule for the world's reef-building corals).

3.2.8. Sea-level Rise (Factor E)

Sea-level rise refers to the ongoing increase in mean sea-levels around the world resulting from anthropogenic ocean warming. The importance of sea-level rise to the extinction risk of the world's reef-building corals was rated as "Low-Medium" in the 2014 final listing rule (79 FR 53851), as shown in the left columns of Table 2 above. Sea-level rise is summarized here based on the SRR (Brainard et al. 2011), the 2014 final listing rule (79 FR 53851), and new information that has become available since then, in terms of: (1) observed sea-level rise to date within the Indo-Pacific; (2) projected sea-level rise within the Indo-Pacific in the foreseeable future (i.e., from now to 2100); (3) observed effects of sea-level rise on Indo-Pacific reef coral communities to date; and (4) projected effects of sea-level rise on Indo-Pacific reef coral communities in the foreseeable future.

Observed Sea-level Rise. Global mean sea level rose faster in the 20th century than in any prior century over the last three millennia, with a 20 cm rise over the period 1901–2018. Sea-level rise has accelerated since the late 1960s, with an average rate of 0.23 cm annually over the period 1971–2018 increasing to 0.37 cm annually over the period 2006–2018 (IPCC 2022). Sea-level rise is not spatially uniform, with portions of the Indo-Pacific such as Tuvalu and Tokelau in the western tropical Pacific Ocean experiencing rates of sea-level rise approximately three times faster than the global mean since 1950 (Becker et al. 2012).

Projected Sea-level Rise. Sea-level rise is projected to accelerate in the foreseeable future due to the melting of land and sea ice, combined with thermal expansion. Under SSP2-4.5, AR6 projects total sea-level rise of 56 cm over the period 2022 – 2100 (compared to the 1995–2014 baseline), at a rate of 0.77 cm annually by 2181 – 2100. Under SSP3-7.0, the projections are for 68 cm over the period 2022–2100 at a rate of 1.04 cm annually by 2181–2100 (Table 9.9, IPCC 2022). It is important to note that projected regional sea-level rise differs substantially from the projected global mean for some Indo-Pacific coral reef areas. For example, the Torres Strait and nearshore areas of the northern Indian Ocean are projected to rise less than the projected global mean, whereas areas around the northern Philippines and Hawaii are projected to rise more than the projected global mean (IPCC 2022, Figure 9.28c,d).

Observed Effects of Sea-level Rise. Sea-level rise over the past few decades has resulted in physical impacts in coral reef areas, such as increased coastal erosion and water quality degradation. However, there is little information available on the effects of sea-level rise on Indo-Pacific corals, most likely because the sea-level rise in much of the region so far has been slow and small, making detection of any biological response difficult (Brainard et al. 2011, 79 FR 53851). In those cases where localized sea-level rise has been relatively high, evidence from Indo-Pacific coral responses so far generally show beneficial effects by providing new substrates for corals to colonize (van Woesik et al. 2015, Albert et al. 2017, Chen et al. 2018). However, widespread impacts on Indo-Pacific coral reefs such as increased coastal erosion and water quality degradation are expected to occur in the foreseeable future, due to the much higher projected rates of sea-level rise compared to recent decades (Brainard et al. 2011, 79 FR 53851).

Projected Effects of Sea-level Rise. Under SSP2-4.5 and SSP3-7.0, rates of mean global sea-level rise of 0.77 and 1.04 cm annually are projected to occur by 2081–2100 (IPCC 2022). Many studies show that that these projected rates of sea-level rise are likely to exceed reef accretion rates at that time in the Indo-Pacific (e.g., van Woesik et al. 2015, van Woesik and Cacciapaglia 2018, Perry et al. 2018, Zuo et al. 2021). That is, sea-level rise will be accelerating at the same time that reef accretion is slowing down due to ocean warming, ocean acidification, and other threats, eventually leading to submergence of reefs below depths needed for adequate light. In addition, sea-level rise is projected to impact Indo-Pacific coral reefs via increased sedimentation due to increased coastal erosion (Bramante et al. 2020), and degradation of water quality by wastewater leakage (McKenzie et al. 2021). Thus, sea-level rise is likely to impact Indo-Pacific coral reefs in the foreseeable future in several ways, including reef submergence as reef accretion rates decline, sedimentation from coastal erosion, and degradation of water quality.

Sea-level Rise Conclusion. Based on the above summaries and cited information, we conclude that: (1) the rate of sea-level rise has been gradually increasing in recent decades, and the rate of change since 2014 may have been too gradual to result in measurable effects on corals; and (2) the rate of sea-level rise is projected to accelerate in the foreseeable future under SSP2-4.5 and SSP3-7.0, especially in the latter half of the 21st century, gradually impacting Indo-Pacific corals by reef submergence as reef accretion rates decline, sedimentation from coastal erosion, and degradation of water quality. Thus, we rate the current importance of sea-level rise to the extinction risk of

Indo-Pacific reef-building corals as "Low," as shown in the right columns of Table 2 above (down from "Low-Medium" in the 2014 final rule for the world's reef-building corals).

3.2.9. Inadequacy of Existing Regulatory Mechanisms (Factor D)

Existing regulatory mechanisms refers to treaties, agreements, laws, and regulations at all levels of government that may affect the continued existence of reef-building corals. The inadequacy of existing regulatory mechanisms is not included in the above list of threats because it does not constitute physical or biological conditions that directly threaten reef-building corals. Relevant regulatory mechanisms include numerous treaties, agreements, laws, and regulations at the international, national, state, local, and other levels, thus their collective effects cannot be observed or projected like the direct threats. Nonetheless, they are included in the Threats Evaluation because we must evaluate the inadequacy of existing regulatory mechanisms under ESA section 4(a)(1). Hence, in support of the 2014 final coral listing rule (79 FR 53851), a Management Report was developed to identify existing regulatory mechanisms and conservation efforts relevant to threats to the direct threats to Indo-Pacific reef-building coral species that were being considered for listing (NMFS 2012). The report covers regulatory mechanisms relevant to addressing both global and local threats, i.e., GHG management globally and the management of local threats in the 68 countries with Indo-Pacific reef-building corals. This section summarizes information from that report (NMFS 2012), the final coral listing rule (79 FR 53851), and more recently available information.

GHG Management. Greenhouse gases (GHGs) are regulated through international agreements and through statutes and regulations at the national, state, and local levels. The major international agreements to manage GHGs are: (1) The binding Montreal Protocol of 1987 with eight subsequent revisions between 1990 and 2016 to protect the stratospheric ozone layer by phasing out the production and consumption of ozone-depleting substances (which are also secondary GHGs); (2) the 1992 United Nations Framework Convention on Climate Change (UNFCCC) to "stabilize greenhouse gas concentrations in the atmosphere at a level that would prevent dangerous anthropogenic interference with the climate system," which establishes how international treaties may be negotiated to reduce emissions of the primary GHGs (CO_2, methane, nitrous oxide, and others); (3) the binding Kyoto Protocol of 1997 to implement the UNFCCC by reducing CO_2, methane, nitrous oxide, and other GHGs to 1990 levels by 2012 (although the Kyoto Protocol covered only a small fraction of global emissions because many of the major GHG emitters were not signatories); (4) as an interim replacement to the Kyoto Protocol, the non-binding 2009 Copenhagen Accord to limit the increase in average global temperature to 2°C above the pre-industrial level by implementing national GHG reductions starting in 2020; and (5) as a permanent replacement to the Kyoto Protocol, the binding 2015 Paris Agreement (UN 2015), which was signed in 2016 by 195 UNFCCC member countries (UN 2016) with the objective of "holding the increase in the global average temperature to well below 2°C above pre-industrial levels and to pursue efforts to limit the temperature increase to 1.5°C above pre-industrial levels" by implementing policies to reduce national GHG emissions starting in 2020 (NMFS 2012, 2014, 2020; UN 2015, 2016).

The Montreal Protocol successfully reduced ozone-depleting substances, leading to recovery of the ozone layer and a modest reduction in secondary GHGs (NMFS 2012). However, the Kyoto Protocol has not been effective at controlling global GHG emissions, because many of the top GHG emitters did not sign the protocol, and some who did were unable to ratify the protocol or implement it as intended. As a result, atmospheric CO_2 concentrations increased from approximately 360 ppm to 390 ppm during the time the protocol was in effect from 1997 to 2012 (https://www.esrl.noaa.gov/gmd/ccgg/trends/, accessed August 2022), due to the steady increase in GHG emissions during that time (IPCC 2013, IEA 2018). The Copenhagen Accord represented some progress but was only intended as a non-binding interim step until a more permanent binding agreement could be completed, which was accomplished with the Paris Agreement.

Each of the 195 signatories of the Paris Agreement is required to develop "Nationally Determined Contributions" (NDCs) under the agreement that specify national GHG reduction targets and how they will be met. All 195 signatory countries submitted NDCs to the UNFCCC by 2021 (https://www4.unfccc.int/sites/ndcstaging/Pages/Home.aspx, accessed August 2022). Although nearly all countries in the world signed the Paris Agreement in 2016, and all 195 signatory countries have submitted their NDCs, these NDCs have not yet led to GHG emissions management policies adequate to meet the Paris Agreement: UNEP's annual Emissions Gap Reports monitor the implementation of the Paris Agreement, and as shown in Figure 4 in Section 2.1 above, current GHG emissions management policies (as of December 2021) are likely to result in global warming of 2.6-3.4°C above pre-industrial by 2100 (UNEP 2021a).

Since 2018, most of the world's countries have committed to net zero GHG emissions goals by mid-century (mostly 2050, but ranging from 2030 to 2060), including the United States. As of December 2021, 136 countries had net zero goals, representing the majority of global GHG emissions. UNEP's model projects that if all net zero targets were to be met by mid-century, global warming is likely to be limited to 2.0–2.7°C above pre-industrial by 2100 (UNEP 2021a), as shown in Figure 4 in Section 2.1 above.

Even if implementation of the Paris Agreement successfully limits global warming to 1.5°C above pre-industrial by 2100 as intended (i.e., <0.5°C of additional warming above current levels), this would result in substantial degradation of the world's coral reefs above what has occurred so far (Hughes et al. 2017b, Lough et al. 2018). That is, severe impacts are anticipated from only an additional <0.5°C of warming above current levels because coral reefs are already on a downward trajectory, and the additional warming would make things worse (IPCC 2018, 2022). In conclusion, while meeting the objective of the Paris Agreement would obviously be a great improvement over the trajectory from current policies, much more than that is necessary for recovery of the 15 listed coral species.

Local Threats Management. Existing regulatory mechanisms that address the major local threats to reef-building corals (i.e., fishing, LBSP, disease, coral predators, collection and trade) consist primarily of national and local fisheries, coastal, and watershed management laws and regulations in the 68 countries where Indo-Pacific reef-building corals occur, but also include some international conventions. Regulatory mechanisms align well with some threats (e.g., fishing, collection and trade) but not others (e.g., disease and predators). The relevant regulatory mechanisms generally consist of five categories: General coral protection, coral collection control, fishing controls, pollution controls, and managed areas, as summarized below. These regulatory mechanisms do not address climate change threats, but they typically were not intended to do so (NMFS 2012, 2014).

General coral protection regulatory mechanisms include overarching environmental laws that may protect corals from damage, harm, and destruction, and specific coral reef management laws. In some instances, these general coral protection regulatory mechanisms are limited in scope because they apply only to certain areas or only regulate coral reef damage and do not prohibit it completely. Of the 68 countries, 18 (26%) have general coral protection laws. In addition, some international regulatory mechanisms help protect corals and coral reefs, such as the Convention on Biological Diversity (signed in 1992 to promote conservation of biological diversity), and the Ramsar Convention (signed in 1971 to conserve wetlands and nearshore habitats). These diverse national and international regulatory mechanisms are intended to protect coral reefs in various ways, such as by requiring compensation for destruction and damage of coral reefs (e.g., ship groundings), prohibiting or regulating development near coral reefs, and other means. Some of these regulatory mechanisms indirectly reduce the threat of LBSP by reducing the amount of development near coral reefs, thereby reducing runoff of sediment and nutrients. However, in many countries and locales, the laws are not well enforced (NMFS 2012, 2014).

Coral collection and trade regulatory mechanisms include specific laws that prohibit the collection, harvest, and mining of corals. In some instances, these coral collection regulatory mechanisms are limited in scope because they apply only to certain areas, or are regulated but not prohibited. Of the 68 countries, 32 (47%) have laws prohibiting the collection of live corals from coral reefs. In addition, at least one international regulatory mechanism helps reduce the collection of live corals (CITES), which prohibits or restricts trade of species listed in any of its three categories. Nearly all reef-building corals are listed in CITES Appendix II, which requires regulation and tracking of international trade to avoid utilization incompatible with their survival (see Collection and Trade section above). However, CITES vastly undercounts international trade of many corals (likely including many listed species) because it does not require identification to species, among other reasons (CBD 2021). These national and international regulatory mechanisms address the threat of collection and trade, but in many countries and locales, the laws are not well enforced (NMFS 2012, 2014).

Fishing regulations that pertain to reefs include regulations that prohibit explosives, poisons and chemicals, electrocution, spearfishing, specific mesh sizes of nets, or other fishing gear. Fisheries management regimes regulate reef fishing in many parts of the collective ranges of these coral species, albeit at varying levels of success. Of the 68 countries, 53 (68%) have laws that regulate coral reef fisheries. Although these laws are very diverse, they all prohibit destructive fishing practices, especially the use of dynamite or otherwise deconstructing the reef, while many also prohibit the use of poisons. Many of the 53 countries entirely prohibit spearfishing while scuba diving at night when reef fish are much more vulnerable. Some of the 53 countries prohibit or regulate fishing nets and traps on coral reefs. These national regulatory mechanisms address the threat of fishing, but in many countries and locales, the laws are not well enforced. We were unable to identify any international regulatory mechanism that address coral reef fisheries (NMFS 2012, 2014).

Pollution control regulations include oil pollution laws, marine pollution laws, ship-based pollution laws, and coastal land use and development laws. Of the 68 countries, 23 (34%) have laws that regulate pollution of coral reef waters. In addition, some international regulatory mechanisms are intended to protect coral reefs from pollution, such as the International Convention for the Prevention of Pollution from Ships (MARPOL, signed in 1973) and the Ramsar Convention. These national and international regulatory mechanisms address both marine-based and LBSP by reducing the amount of toxins, sediment, nutrients, and other pollutants entering coral reef waters, thereby directly addressing the threat of LBSP. These laws also indirectly address the threats of disease and predators, which are exacerbated by toxins, sediment, nutrients, and other pollutants. They are generally less effective than those regulating fisheries or collection and trade, because sources of pollution are usually spread out over large watershed and coastal areas, thus much more difficult to regulate. In addition, in many countries and locales, the laws are not well enforced (NMFS 2012, 2014). In some jurisdictions (e.g., Hawaii and Palau in 2020), laws have been passed to prohibit the use of sunscreens containing oxybenzone and other harmful chemicals.

Managed area regulatory mechanisms include the capacity to create national parks and reserves, sanctuaries, and marine protected areas (NMFS 2012, 2014). As of 2011, coral reef marine protected areas (MPAs) included approximately 25% of Indo-Pacific coral reefs (Burke et al. 2011), thereby reducing some threats through regulation or banning of fishing, coastal development, and other activities contributing to local threats. Since then, many new MPAs have been established that either greatly restrict or entirely ban fishing and coastal development around Indo-Pacific coral reefs, including large MPAs in Palau, the Cook Islands, New Caledonia, the Seychelles, Indonesia, and elsewhere (Lewis et al. 2017, MPA News 2018, Williams et al. 2019, Campbell et al. 2020, Commonwealth Blue Charter 2021), as shown in the Atlas of Marine Protection https://old.mpatlas.org/map/mpas/, accessed August 2022). While increasing the proportion of Indo-Pacific coral reefs within MPAs is a positive step, inclusion in MPAs does not guarantee that coral reefs are protected from local threats: Only about 15% of MPAs with Indo-Pacific coral reefs were rated as "effective" at protecting the coral reefs within them from local threats in 2010 (Burke et al. 2011), and MPAs are generally not very effective at protecting coral reefs from climate change threats (Bruno et al. 2019).

Regulatory Mechanisms Conclusion. The 2014 final listing rule concluded that global regulatory mechanisms for GHG emissions management were ineffective at reducing global climate change-related impacts to Indo-Pacific reef-building coral species at that time, and therefore inadequate for mitigating climate-related threats to the 15 listed species (79 FR 53851). Since then, the 2015 Paris Agreement was signed by 195 countries, representing a major potential advance in GHG emissions management because its successful implementation would limit GMST to 1.5°C above pre-industrial, as explained in the Global Climate Change section above, and in IPCC's 1.5°C Report (IPCC 2018). However, optimism about the successful implementation of the Paris Agreement is dampened by several facts: (1) despite past international agreements for GHG emissions management (e.g., 1997 Kyoto Protocol, 2009 Copenhagen Accord), global GHG emissions and atmospheric CO_2 levels have both risen to historically high levels and continue to rise; (2) the U.S.'s (the world's second largest GHG emitter) withdrawal in 2020 and rejoining in 2021 demonstrated how politics can interfere with implementation; and (3) recent analyses show that many of the G20 nations are falling short of the commitments they made in the Paris Agreement (UNEP 2018, 2019, 2020, 2021a). Finally, even successful implementation of the Paris Agreement would result in a worsening of the current conditions, as explained in the Ocean Warming section above. Thus, we conclude that while current global regulatory mechanisms for management of GHG emissions (i.e., the Paris Agreements and subsequent national policies) have recently substantially improved, they are still grossly inadequate for the conservation of Indo-Pacific reef-building corals including the 15 listed species. Furthermore, while many nations and sub-national jurisdictions recognize the need to manage GHGs and some nations have made great progress, history suggests that collective GHG regulatory mechanisms globally will be inadequate to control any of the threats in the foreseeable future.

The 2014 final listing rule concluded that regulatory mechanisms across the Indo-Pacific were inadequate for controlling local threats to Indo-Pacific reef-building coral species including the 15 listed species at that time (79 FR 53851). Since then, many new MPAs have been established that either greatly restrict or entirely ban fishing and coastal development around Indo-Pacific coral reefs, including MPAs that encompass entire archipelagos, although inclusion in MPAs does not guarantee that coral reefs are protected from local threats. However, overall there has been little change since 2014 in regulatory mechanisms for local threats. Thus, we conclude that while there has been some progress with regulatory mechanisms for local threats (i.e., establishment of MPAs), they are still inadequate for the conservation of Indo-Pacific reef-building corals including the 15 listed species. Furthermore, while many nations and sub-national jurisdictions recognize the need to manage local threats and some nations have made great progress, historical information suggests that regulatory mechanisms for local threats will continue to be inadequate to control any of the threats in the foreseeable future.

The 2014 final listing rule (79 FR 53851) did not provide a relative rating of the importance of the inadequacy of existing regulatory mechanisms to the extinction risk of the world's reef-building corals, although the Management Report (NMFS 2012) and the final rule both emphasized its central importance. Adequate regulatory mechanisms are required to control each threat, whether directly or indirectly (e.g., adequate GHG management would directly control ocean warming and indirectly control disease), and thus we rate the relative importance of the inadequacy of existing regulatory mechanisms to the extinction risk of the world's reef-building corals as "High".

3.3. Threats Evaluation Conclusion

The general threats evaluation in the 2014 final listing rule (79 FR 53851) was for the world's reef-building corals based on the best available information available at that time, whereas this one is limited to Indo-Pacific reef-building corals based on currently available information. As noted in the introduction to the threats evaluation, this led to some changes in the definitions of two of the threats (fishing and LBSP), as well as changes to the relative importance ratings of five of the threats to the extinction risk of Indo-Pacific reef-building corals: ocean warming was changed from High to Very High, ocean acidification was changed from Medium-High to High, Predation and Collection and Trade were both changed from Low to Low-Medium, and sea-level rise was changed from Low-Medium to Low. The rationales for these changes to the threat definitions and importance ratings are provided in the threats sub-sections, and the relative importance ratings for the threats are shown in Table 3 below.

In conclusion, the best available current information indicates that ocean warming, ocean acidification, disease, and predation have all worsened since the 15 corals were listed in 2014, especially the most important threat to Indo-Pacific reef-building corals, ocean warming and warming-induced bleaching. All threats are projected to worsen in the foreseeable future under SSP2-4.5 or SSP3-7.0, with ocean warming and ocean acidification projected to greatly worsen, while disease, fishing, LBSP, predation, and collection and trade projected to substantially worsen (Table 3).

Although the Paris Agreement represents progress in global GHG management, ocean warming and ocean acidification would likely continue to worsen throughout the 21st century even if the agreement is successfully implemented, including achieving net zero targets. That is, additional regulatory mechanisms for GHG management are necessary to control these threats to reef-building corals adequately. Likewise, while progress has been made in many countries on controlling local threats, all are expected to continue to worsen unless additional regulatory mechanisms and conservation efforts are put into place (Table 3).

Table 3. Summary of general threats evaluation for Indo-Pacific reef-building corals. For each threat, importance to the extinction risk of the species, observed trend since 2014, and projected trend in the foreseeable future are provided.

Threat (listing factor)	Importance Rating	Observed Trend in Effects of Threat Since 2014	Projected Trend in Effects of Threat Under SSP2-4.5 and SSP3-7.0 by 2100
Ocean Warming (Factor E)	Very High	Effects have substantially worsened, mainly due to the series of mass coral bleaching events across the Indo-Pacific in 2014-17, the most severe and widespread on record.	Effects are projected to greatly worsen under either scenario, even assuming broad coral adaptation capacity.
Ocean Acidification (Factor E)	High	Effects have worsened, as shown by decreased coral and crustose coralline algae calcification rates and increased reef erosion rates.	Effects are projected to greatly worsen under either scenario, especially in terms of interactions with other threats.
Disease (Factor C)	High	Effects have worsened, especially because the 2014-17 bleaching events increased stressors on corals that lead to disease.	Effects are projected to substantially worsen under either scenario, as stressors leading to disease increase.
Fishing (Factor A)	Medium	Direct and indirect effects have continued, likely intensifying in some locations while lessening in others due to various factors.	Effects are projected to substantially worsen under either scenario, as population pressure and interactions with other threats rise.
LBSP (Factors A and E)	Low-Medium	Effects have continued, likely intensifying in some locations while lessening in others due to various factors.	Effects are projected to substantially worsen under either scenario, as population pressure and interactions with other threats rise.
Predation (Factor C)	Low-Medium	Effects have worsened, mainly because the 2014-17 bleaching events resulted in more favorable conditions for predators such as COTS.	Effects are projected to substantially worsen under either scenario, as other threats lead to increasingly favorable conditions for predators.
Collection and Trade (Factor B)	Low-Medium	Effects have continued, but information is inadequate to determine overall trends.	Effects are projected to substantially worsen under either scenario, from simultaneous increases in demand and interactions with other threats.
Sea-level Rise (Factor E)	Low	No detectable trends.	Minimal effects over the next few decades but projected to eventually worsen under either scenario
Inadequacy of Existing Regulatory Mechanisms (Factor D)	High	Some progress especially for GHG management but generally inadequate for all threats.	Additional progress projected but still likely to be inadequate for all threats.

4. Species Reports

The following 15 species reports are based on the SRR (Brainard et al. 2011), the 2014 final listing rule (79 FR 53851), pre-2014 information that was not included in either document, and new information that has become available since 2014. For each species, the information is organized in terms of background, distribution, abundance, threats, and the conclusion. The Background section provides important contextual information for the species, including taxonomy, morphology, habitat and life history. The Distribution section summarizes the species' geographic and depth distributions which together provide its overall distribution, and explains the relevance of overall distribution to the status of the species. The Abundance section describes the species' relative abundance, absolute abundance, and abundance trends, and explains the relevance of abundance to the status of the species. The Threats section describes the impacts of each threat on the species, summarized in a table. The Conclusion summarizes the new information that has become available since 2014, and provides our determination of the current status of the species based on the information presented in the species report.

4.1. *Acropora globiceps* (Dana 1846)

4.1.1. Biology

Taxonomy. The species was originally described as *Madrepora globiceps* (Dana 1846), then assigned to the genus *Acropora* (Verrill 1902). The similar species *Madrepora humilis* was also described by Dana (1846), and assigned to the genus *Acropora* (Verrill 1902). Wells (1954) included 17 nominal species in his synonymy of *A. humilis*, separated into three "formae" or growth forms (α, β, γ). Forma β included *A. humilis*, *A. globiceps*, and eight other nominal species (Wells 1954), which was supported by Veron and Wallace (1984). That is, Wells (1954) and Veron and Wallace (1984) lumped *A. globiceps* under *A. humilis*. This is reflected in the primary coral taxonomic literature of that time, which included *A. humilis* but not *A. globiceps* (e.g., Scheer and Pillai 1974, Wallace 1978, Randall and Myers 1983, Nemenzo 1986, Veron 1986). However, as explained in Wallace's worldwide revision of the genus *Acropora* (Wallace 1999), *A. globiceps* is the correct name for a suite of specimens with distinctive characters, which was supported by Wallace et al.'s (2012) additional revision of the genus *Acropora*. The name *A. globiceps* is used in the Corals of the World books (Veron 2000) and website (http://www.coralsoftheworld.org/, accessed August 2022), has been widely used in recent years (e.g., Brainard et al. 2011, Adjeroud et al. 2015, DeVantier and Turak 2017), and is accepted by the World Register of Marine Species (WoRMS, Hoeksma and Cairns 2021).

Morphology. Colonies of *A. globiceps* are typically about 25 cm in diameter or less, but can reach approximately 1 meter (m) in diameter. Colonies are round, with finger-like branches growing upward. Branches are uniform in size and shape, roughly finger length, diameter, and shape, with almost no side branches. The branch tips are rounded, the axial corallites (i.e., the corallite on the end of each branch) are small and short, and the radial corallites (i.e., corallites on the sides of branches) are uniform and fairly small, and often some are in rows. Branches are usually close together and can have a narrow, uniform crack between them, though not always. The length of branches, how close they are together, and the degree of branch tapering varies some between colonies, but usually not within colonies. Colony color is typically cream to brown, and sometimes fluorescent green in some locations (Fig. 5). *Acropora globiceps* is similar to some other *Acropora* species such as *A. humilis*, but has distinctive characteristics and can be reliably identified in the field, as noted above and in more detail in Fenner and Burdick (2016) and Fenner (2020a).

Figure 5. *Acropora globiceps*, showing colony and branch morphology. Upper right photo is from Rota, Commonwealth of the Northern Mariana Islands, and the others are from Tutuila, American Samoa (photos copyright, Doug Fenner).

Habitat. *Acropora globiceps* is typically found on shallow forereefs, but may also occur in backreef areas such as the outer margins of reef flats, and within pools and lagoons where wave energy is high (NMFS 2022b). The Coral Traits Database (https://coraltraits.org/, accessed August 2022) lists *A. globicep*'s water clarity preference as "clear", and wave exposure preference as "exposed".

Life History. Little information is available on the life history of *A. globiceps*. Generally, *Acropora* species have rapid skeletal growth and low tolerance to stress, and all are hermaphroditic (same colony produces eggs and sperm) broadcast spawners (Brainard et al. 2011). Darling et al. (2012) performed a biological trait-based analysis to categorize 143 of the world's reef-building coral species into 4 life history strategies: generalist, weedy, competitive, and stress-tolerant. All 37 of the *Acropora* species in the study (which did not include *A. globiceps*) were classified as "competitive species", based on broadcast spawning, rapid skeletal growth, and branching colony morphology. These life history characteristics allow *Acropora* species to recruit quickly to available substrate and successfully compete for space, but also make them susceptible to disturbance, thus they typically are only dominant in ideal conditions (Darling et al. 2012). In French Polynesia, *A. globiceps* populations are frequently disturbed by warming-induced bleaching, storms, and other threats, resulting in high levels of mortality, rapid turnover, and high proportions of small colonies (Adjeroud et al. 2015, Kayal et al. 2015).

4.1.2. Distribution

Geographic Distribution. As explained in Section 1.1, this document uses Spalding et al.'s (2007) Marine Ecoregions of the World (MEOWs) and provinces to portray the geographic distributions of the 15 listed coral species. The combined distributions of the 15 listed corals occur in a total of 76

MEOWs within 26 provinces, as shown in Figures 2 and 3 in section 1. *Acropora globiceps* has a relatively broad distribution (the most broadly distributed of the 15 species reviewed in this document), occurring in 39 (Fig. 6) of those 76 MEOWs, based on information in NMFS (2022c). The distribution of the species within U.S. waters is summarized below. The current information indicates that *A. globiceps* occurs in four more MEOWs than we were aware of at the time of listing in 2014, including the Chagos, Hawaii, Johnston Atoll, and Phoenix/Tokelau/Northern Cook Islands MEOWs (NMFS 2022c). Occurrence in both the central Indian Ocean (Chagos) and northeastern Pacific Ocean (Hawaii) indicates that the species' geographic distribution is considerably larger than previously known.

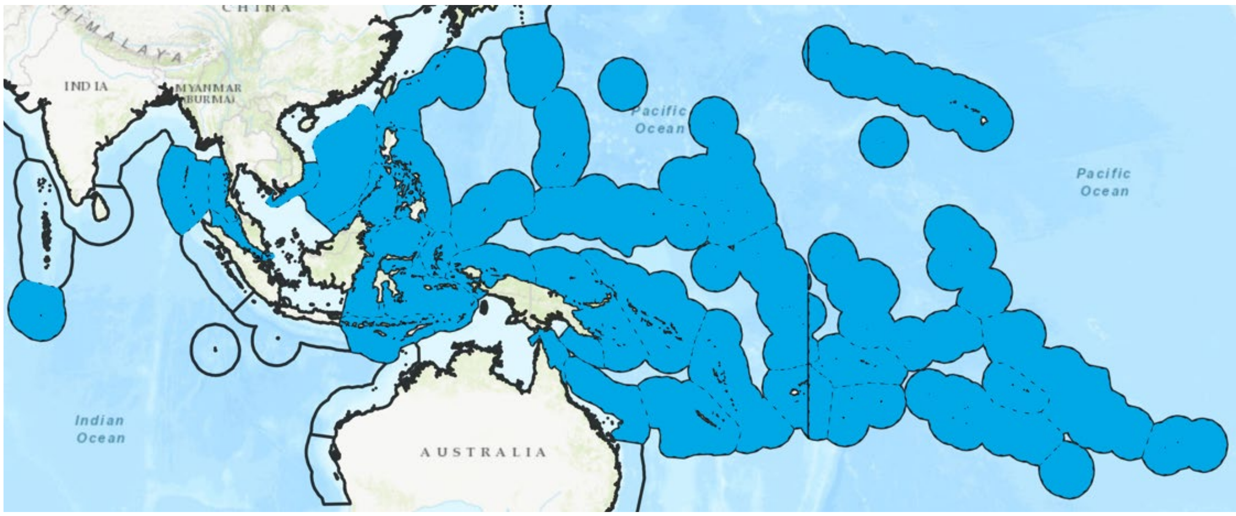


Figure 6. Geographic distribution of *A. globiceps*.

Depth Distribution. *Acropora globiceps* has a relatively moderate depth distribution ranging from 0 – 20 m, although it is typically more abundant at <8 m depth (NMFS 2022b, Coral Traits Database https://coraltraits.org/, accessed August 2022). Thus, current information indicates that *A. globiceps* has more than a twice as large depth range (0–20 m) than we were aware of at the time of listing in 2014 (<8 m).

U.S. Distribution. *Acropora globiceps* is the most widely-distributed ESA-listed coral species within U.S. waters. It occurs on Guam (a single island), the Commonwealth of the Northern Mariana Islands (CNMI, an archipelago of 15 islands), American Samoa (an archipelago of 7 islands), the Pacific Remote Island Areas (PRIA, an administrative grouping of 7 islands, atolls, and reefs widely distributed across the central Pacific), and the Northwestern Hawaiian Islands, as described in more detail in NMFS (2022b). Guam and CNMI are within the Mariana Islands MEOW, American Samoa is within the Samoa MEOW, PRIA is distributed across several MEOWs, and the Northwestern Hawaiian Islands are within the Hawaii MEOW (Spalding et al. 2007).

On Guam, *A. globiceps* is widely distributed on the reef slopes around the island. In CNMI, the species is also widely distributed around the larger islands, including Rota, Tinian, Saipan, and Pagan, and also occurs on Aguijan, Farallon de Medinilla, Alamagan, the Maug Islands, and Uracas (NMFS 2022b). In American Samoa, *A. globiceps* is widely distributed on the reef slopes around Tutuila. The species also occurs on most of the smaller islands, including Ofu, Olosega, Ta'u, and Rose Atoll. In PRIA, *A. globiceps* occurs on Palmyra, Johnston and Wake Atolls. In Hawaii, *A. globiceps* occurs on French Frigate Shoals in the Northwestern Hawaiian Islands (NMFS 2022b).

Relevance of Distribution to Status. Geographic and depth distributions were the key spatial factors considered in determining the status of coral species and in the listing of *A. globiceps* in 2014. A narrow geographic or depth distribution exacerbates a species' extinction risk because larger proportions of the population are likely to be exposed to any single disturbance. In contrast, a broad overall distribution moderates a species' extinction risk because the population is distributed across a range of geographic areas and depths, and thus lower proportions of the populations are likely to be exposed to any single disturbance. For example, one reason that *A. globiceps* was listed was because the information available at that time indicated a narrow depth distribution of 0–8 m (79 FR 53851). Since both the geographic and depth distributions of *A. globiceps* are greater than we were aware of at the time of listing in 2014, its distribution has a greater capacity to moderate extinction risk.

4.1.3. Abundance

Relative Abundance. Relative abundance refers to how common *A. globiceps* is compared to other reef-building coral species. DeVantier and Turak (2017) published a large study on the abundances of over 600 species of Indo-Pacific reef-building corals at a total of 3,075 sites in 31 Veron ecoregions (Veron et al. 2015, 2016) spanning much of the Indo-Pacific from the Red Sea to Fiji, based on survey data collected from 1994 to 2016. Surveys were generally conducted between the surface and approximately 40 m of depth, although some extended to 40–50 m. For each species, occurrence (percentage of sites in which that species was present) and mean abundance (sum of individual site abundance scores divided by the number of sites in which that species was present) were used to quantify overall abundance on a scale of 0–500, then the following categories were used to characterize relative abundance: <0.1 = Very Rare; 0.1–<1.0 = Rare; 1.0–<10.0 = Uncommon; 10.0–<50.0 = Common; 50–<100 = Very Common; 100–500 = Near Ubiquitous (DeVantier and Turak 2017).

Acropora globiceps was recorded in 13 of the 31 ecoregions. Within those 13 ecoregions, it had a mean overall abundance of 17.63 (Common), ranging from 1.21 (Uncommon) in the Lesser Sunda Islands and Savu Sea Ecoregion to 100.00 (Near Ubiquitous) in the Yap Islands, Micronesia Ecoregion. The mean overall abundance of *A. globiceps* for all 31 ecoregions was 6.08 (Uncommon, DeVantier and Turak 2017, Table S2), however some of the 18 ecoregions where it was not recorded may be outside its range. The Coral Traits Database (https://coraltraits.org/, accessed August 2022) lists *A. globiceps*'s global relative abundance as "common," but does not cite DeVantier and Turak (2017). In French Polynesia (outside the area surveyed by DeVantier and Turak 2017), *A. globiceps* is one of the most common reef coral species (Adjeroud et al. 2015, Burkepile et al. 2020). Within its range, the relative abundance of *A. globiceps* may vary locally from very rare to near ubiquitous. However, based on the above information, the rangewide relative abundance of *A. globiceps* is uncommon to common.

Absolute Abundance. Absolute abundance is an estimate of the total number of colonies of a species that currently exists throughout its range. *Acropora globiceps* has been estimated to have an absolute abundance of at least tens of millions of colonies (79 FR 53851). Dietzel et al. (2021) estimated its absolute abundance at 654 million colonies. Muir et al. (2022) argued that the data were unsuitable to provide such quantitative estimates, and Dietzel et al.'s (2022) reply agreed that better data are needed. Swanson (2019) estimated the absolute abundance of *A. globiceps* in the Mariana Islands alone at 3 million adult colonies, an archipelago of only 15 small islands. Some individual MEOWs within *A. globiceps*'s range, such as the Eastern Philippines, Lesser Sunda, and Solomon Archipelago MEOWs, encompass over 500 islands each, and the species' range of 39 MEOWs includes at least 10,000 islands (Spalding et al. 2007, Veron et al. 2016). Based on the updated information, *A. globiceps*' absolute abundance is likely to be at least hundreds of millions of colonies. Thus, current information indicates that *A. globiceps* has a higher absolute abundance (at least hundreds of millions) than we were aware of at the time of listing in 2014 (at least tens of millions).

Abundance Trends. When *A. globiceps* was listed in 2014, it was thought to have a decreasing abundance trend across its range over at least the past several decades, based on overall declines in coral cover and the susceptibility of *A. globiceps* to the worst threats. At that time, we were not aware of any time-series abundance trend data for this species (79 FR 53851). Since then, we learned of the National Park of American Samoa's (NPSA) coral species monitoring surveys conducted annually at 15 fixed and 15 temporary transects at 10–20 m depth from 2007 to 2019 on the north shore of Tutuila. On the fixed transects, *A. globiceps* cover ranged from zero to approximately 0.20% cover annually, with an increasing trend. On the temporary transects, it ranged from zero to approximately 0.40% cover annually, with no apparent trend (NPSA 2020). The monitoring program is designed to monitor coral cover trends on the spatial scale of NPSA's Tutuila Unit (i.e., reef scale), and may or may not reflect abundance trends on larger spatial scales, such as island, archipelago or MEOW scales.

As described above in the general Threats Evaluation and below for threats to *A. globiceps*, the most important threats (i.e., ocean warming, ocean acidification) have worsened since 2014, and substantial impacts to *Acropora* species including *A. globiceps* have been documented. Based on the continued worsening in the most important threats, it is likely that *A. globiceps* is decreasing in overall abundance (i.e., abundance across all the ecoregions that make up its range).

Relevance of Abundance to Status. Abundance is the key demographic factor considered in determining the status of coral species and in the listing of *A. globiceps* in 2014. A low relative or absolute abundance, especially in combination with declining abundance, exacerbates a species' extinction risk because larger proportions of the population are likely to be exposed to any single disturbance. In contrast, a higher relative or absolute abundance moderates a species' extinction risk because lower proportions of the population are likely to be exposed to any single disturbance (79 FR 53851). Since the absolute abundance of *A. globiceps* is greater than we were aware of in at the time of listing in 2014, its abundance may have a greater capacity to moderate extinction risk.

4.1.4. Threats

This section provides an updated threats evaluation for *A. globiceps*, focusing on the threats that contributed to its listing (79 FR 53851), including ocean warming, ocean acidification, disease, fishing, LBSP, predation, and inadequacy of existing regulatory mechanisms. In addition, current information indicates that collection and trade is also impacting the status of the species. A threats summary table is provided, including relative importance ratings for the threats, effects of threats since listing in 2014, and projected effects of threats in the foreseeable future.

Ocean Warming: As noted in Section 3.2.1 above, since listing in 2014, the effects of ocean warming on Indo-Pacific reef-building corals have substantially worsened. In response to the 2014–2017 series of warming-induced bleaching events, *Acropora* corals were generally the most impacted coral taxa in different locations around the Indo-Pacific (e.g., Hoogenboom et al. 2017, Frade et al 2018, Hughes et al. 2018a,b, Raymundo et al. 2019, Thinesh et al. 2019, Dietzel et al. 2020, Gilmour et al. 2022). Section 3.2.1 also describes how ocean warming is projected to greatly worsen in the foreseeable future (i.e., between now and 2100).

With regard to impacts of this threat on *A. globiceps*, on Guam in the Mariana Islands, a series of warming-induced bleaching events resulted in a sharp reduction in the mean *Acropora* cover on the forereefs, and mortality of *A. globiceps* colonies from bleaching was higher than overall coral mortality from bleaching (Raymundo et al. 2019). On Kiritimati (Christmas) Atoll in the Line Islands of Kiribati, virtually all *A. globiceps* colonies in the lagoon were killed by the 2016 warming-induced bleaching event (Bowden-Kerby et al. 2021). On Moorea in French Polynesia, the largest, most fecund coral colonies of *Acropora* species including *A. globiceps* had disproportionately high mortality in response to a warming event in 2019 (Speare et al. 2022). In conclusion, the current information indicates that *A. globiceps* continues to be highly susceptible to ocean warming, that this threat has substantially worsened since listing in 2014, and that it will greatly worsen in the foreseeable future (Table 4).

Ocean Acidification: As noted in Section 3.2.2 above, since listing in 2014, the effects of ocean acidification on Indo-Pacific reef-building corals have worsened. Generally, *Acropora* species are susceptible to reduced calcification and skeletal growth from ocean acidification (Brainard et al. 2011, 79 FR 53851, Smith et al. 2020, Evenson et al. 2021, Hill and Hoogenboom 2022). Section 3.2.2 also describes how ocean acidification is projected to greatly worsen in the foreseeable future. In conclusion, the current information indicates that *A. globiceps* continues to be susceptible to ocean acidification, that this threat has worsened since listing in 2014, and that it will greatly worsen in the foreseeable future (Table 4).

Disease: As noted in Section 3.2.3 above, since listing in 2014, the effects of disease on Indo-Pacific corals have increased, mainly in response to the 2014–2017 bleaching events. Generally, *Acropora* species are susceptible to most of the diseases that infect coral, and are more commonly affected by acute and lethal diseases than other corals (Brainard et al. 2011, 79 FR 53851, Hobbs et al. 2015, Aeby et al. 2020, Howells et al. 2020). Section 3.2.3 also describes how disease is projected to substantially worsen in the foreseeable future. In conclusion, the current information indicates that *A. globiceps* continues to be susceptible to disease, that this threat has worsened since listing in 2014, and that it will substantially worsen in the foreseeable future (Table 4).

Fishing: As noted in Section 3.2.4 above, since listing in 2014, the direct and indirect effects of fishing on Indo-Pacific corals have continued, likely intensifying in some locations while lessening in others due to various factors. Generally, branching, fast-growing corals such as most *Acropora* species are susceptible to direct (i.e., damage by fishing gear because of their morphology) and indirect (i.e., increased competition for space with algae) effects of fishing (Brainard et al. 2011, 79 FR 53851). Section 3.2.4 also describes how fishing is projected to substantially worsen in the foreseeable future. In conclusion, the current information indicates that *A. globiceps* continues to be susceptible to fishing, that this threat has continued since listing in 2014, and that it will substantially worsen in the foreseeable future (Table 4).

LBSP: As noted in Section 3.2.5 above, since listing in 2014, the effects of LBSP on Indo-Pacific corals have continued, likely intensifying in some locations while lessening in others due to various factors. Generally, *Acropora* species are relatively susceptible to sediment and nutrients compared to other reef-building coral taxa (Brainard et al. 2011, 79 FR 53851, Carlson et al. 2019, Tuttle and Donahue 2022). Section 3.2.5 also describes how LBSP is projected to substantially worsen in the foreseeable future. In conclusion, the current information indicates that *A. globiceps* continues to be susceptible to LBSP, that this threat has continued since listing in 2014, and that it will substantially worsen in the foreseeable future (Table 4).

Predation: As noted in Section 3.2.6 above, since listing in 2014, the effects of predation on Indo-Pacific corals have increased, mainly because the 2014–2017 bleaching events resulted in more favorable conditions for predators such as COTS. Generally, *Acropora* species are relatively susceptible to predation compared to other reef-building coral taxa (Brainard et al. 2011, 79 FR 53851, Keesing et al. 2019, Tkachenko and Huang 2022). Section 3.2.6 also describes how predation is projected to substantially worsen in the foreseeable future. In conclusion, the current information indicates that *A. globiceps* continues to be susceptible to predation, that this threat has worsened since listing in 2014, and that it will substantially worsen in the foreseeable future (Table 4).

Collection and Trade: Although collection and trade did not contribute to the listing of *A. globiceps* (79 FR 53851), the following information indicates that this threat is likely to be impacting the status of the species. As noted in Section 3.2.7 above, *Acropora* species are relatively susceptible to collection and trade compared to other reef-building coral taxa. According to the CITES database cited in Section 3.2.7, between 1985 and 2017, over 17 million *Acropora* units were globally imported and exported. These units were not identified to species, thus likely included an undeterminable number of unidentified *A. globiceps*. In addition, the database also records that between 2009 and 2017, a total of about 200 *A. globiceps* units were globally imported and exported (NMFS 2022a). Because of the growing popularity of "thick branching" *Acropora* species including *A. globiceps* in the marine aquarium trade (Adams 2015, 2019) as well as the ongoing and projected growth in the industry, collection and trade may increasingly impact the status of *A. globiceps*. Section 3.2.7 also describes how collection and trade is projected to substantially worsen in the foreseeable future. In conclusion, the current information indicates that *A. globiceps* is susceptible to collection and trade, that this threat has continued since listing in 2014, and that it will substantially worsen in the foreseeable future (Table 4).

Sea-level Rise: As noted in Section 3.2.8 above, since listing in 2014, sea-level rise has likely been too gradual to result in measurable effects on Indo-Pacific reef-building corals. In those cases where earthquakes have resulted in substrate uplift resembling sea-level rise, these substrates have been colonized by rapidly-growing corals like *Acropora* species. In conclusion, as in the final rule, the current information indicates that *A. globiceps* is not susceptible to sea-level rise, that there have been no detectable trends in the effects of this threat since listing in 2014, but that it will worsen in the foreseeable future (Table 4).

Regulatory Mechanisms: As noted in Section 3.2.9 above, since listing in 2014, some progress has been made with GHG management as well as controlling local threats although existing regulatory mechanisms are still inadequate to control any of the threats. Section 3.2.9 also describes how it is unlikely that regulatory mechanisms will be improved to the point where they are adequate to control any of the threats in the foreseeable future. In conclusion, the current information indicates that existing regulatory mechanisms remain inadequate to control any threat to *A. globiceps*, and that improvement is unlikely in the foreseeable future (Table 4).

Threats Conclusion for *A. globiceps*: Since *A. globiceps* was listed in 2014, many of the threats to the species have worsened. Especially concerning is that the most important threat to the species, ocean warming, has substantially worsened. In addition, all threats are projected to worsen in the foreseeable future, with the possible exception of regulatory mechanisms, which may continue to improve but also are likely to remain inadequate for controlling any of the threats (Table 4).

Although the final rule rated the relative importance of threats to the world's reef-building corals (Table 2), it did not apply those ratings to *A. globiceps* (79 FR 53851). Instead, the final rule concluded that *A. globiceps* is highly susceptible to ocean warming and susceptible to ocean acidification, disease, fishing, LBSP, and predation, while regulatory mechanisms were inadequate for controlling any threat (79 FR 53851). However, as summarized above, we now have more genus-specific and species-specific information available on the importance of each threat to *Acropora* species and *A. globiceps*, respectively. Based on the general importance ratings of the threats to Indo-Pacific reef-building corals (Table 3) and the genus-specific and species-specific information above, we conclude that the relative importance ratings of each threat to Indo-Pacific corals apply to *A. globiceps*. In addition, the observed threat trends since 2014 and projected threat trends in the foreseeable future are provided (Table 4).

Table 4. Summary of threats evaluation for *A. globiceps*. For each threat, relative importance to the extinction risk of the species, observed trend since 2014, and projected trend in the foreseeable future are provided.

Threat (listing factor)	**Importance**	**Observed Trend in Effects Since 2014**	**Projected Trend in Effects to 2100**
Ocean Warming (Factor E)	Very High	Substantially worsened	Greatly worsen
Ocean Acidification (Factor E)	High	Worsened	Greatly worsen
Disease (Factor C)	High	Worsened	Substantially worsen
Fishing (Factor A)	Medium	Continued	Substantially worsen
LBSP (Factors A and E)	Low-Medium	Continued	Substantially worsen
Predation (Factor C)	Low-Medium	Worsened	Substantially worsen
Collection and Trade (Factor B)	Low-Medium	Continued	Substantially worsen
Sea-level Rise (Factor E)	Low	No detectable trends	Worsen
Inadequacy of Existing Regulatory Mechanisms (Factor D)	High	Some improvement but still inadequate	Improvement but likely still inadequate

4.1.5. Conclusion

As explained in the 2014 final listing rule (79 FR 53851), a species' vulnerability to extinction results from the combination of its spatial (i.e., distribution) and demographic (i.e., abundance) characteristics, threat susceptibilities, and consideration of the baseline environment and future projections of threats. *Acropora globiceps* was listed as threatened in 2014 because of its narrow depth distribution, high susceptibility to ocean warming, susceptibilities to ocean acidification, disease, fishing, LBSP, and predation, inadequate regulatory mechanisms, declining baseline conditions, and projected worsening of threats (79 FR 53851).

Since 2014, we have learned that *A. globiceps* has: (1) a broader geographic distribution (39 MEOWs instead of 35), (2) a broader depth distribution (0–20 m instead of 0–8 m), although it is typically more abundant at <8 m depth; and (3) higher absolute abundance (at least hundreds of millions of colonies instead of at least tens of millions of colonies). That is, *A. globiceps* is more broadly distributed and more abundant than we believed in 2014, and thus may have a higher capacity to moderate the effects of the threats, as explained in the Relevance of Distribution/Abundance to Status sections above.

Since 2014, the effects of ocean warming have substantially worsened, and the effects of most other threats have worsened as well. The extensive bleaching and mortality of *A. globiceps* in response to ocean warming events in 2016 and 2019 confirm its high susceptibility to this threat. All threats are projected to substantially worsen under current global GHG regulatory mechanisms, which would result in global warming of 2.6–3.4°C above the pre-industrial baseline by 2100 (see Fig. 4 in Section 3.1 above). Even if the goal of the Paris Agreement is achieved (i.e., limiting global warming to 1.5°C above pre-industrial by 2100), the threats would become much worse than they are currently (Dixon et al. 2022), likely preventing the recovery of *A. globiceps*. Current regulatory mechanisms are grossly inadequate, especially GHG management.

In conclusion, the above information shows that *A. globiceps* is more broadly distributed and more abundant than we believed in 2014, but that the threats have worsened and that collection and trade is also an important threat to the species. Especially concerning is that the most important threat to the species, ocean warming, has substantially worsened since the species was listed in 2014. The other important threats to the species, including ocean acidification, disease, fishing, LBSP, predation, and collection and trade have also either worsened or continued since 2014. While there has been some progress with regulatory mechanisms, primarily because of the 2016 Paris Agreement, regulatory mechanisms for both global and local threats are still inadequate. However, the species' distribution is broader and its abundance is greater than we were aware of at the time of listing in 2014, both of which are key factors for moderating threats.

4.2. *Acropora jacquelineae* (Wallace 1994)

4.2.1. Biology

Taxonomy. *Acropora jacquelineae* was described by Wallace (1994), with additional taxonomic details provided in more recent publications (Wallace 1999, Wallace et al. 2012). It is included in the Corals of the World books (Veron 2000) and website (http://www.coralsoftheworld.org/, accessed August 2022), and is accepted by WoRMS (Hoeksma and Cairns 2021).

Morphology. Colonies are flat-topped and up to one meter across although usually much smaller, with long, very thin tubular corallites projecting upwards at various angles from branchlets (Fig. 7). There are very few radial corallites in all but the edge of the colony (Wallace 1994, Wallace et al. 2012, Fenner 2020a). Colonies are uniform grey-brown or pinkish in color (Veron 2000, 2016). This species is virtually indistinguishable underwater from *A. speciosa*. The principle difference between these two can only be seen in skeleton under the microscope, whereby *A. jacquelineae* has rows of tiny spines on the outer surface of the corallites, while *A. speciosa* has a dense, evenly-spaced arrangement of spines that are not in rows (Fenner and Burdick 2016, Fenner 2020a). The diameters of the tubular corallites are virtually identical in the two species (Wallace 1999).

Figure 7. *Acropora jacquelineae*, showing colony and branch morphology. Photos from Tutuila, American Samoa (photos copyright, Doug Fenner).

Habitat. *Acropora jacquelineae* occurs on walls and ledges deeper than 10 m (Wallace and Wolstenholme 1998). It is usually more common at 30–50 m depth than <30 m, and is thus considered an upper mesophotic species (Turak and DeVantier 2019). The Coral Traits Database (https://coraltraits.org/, accessed August 2022) lists *A. jacquelineae*'s water clarity preference as "clear," and wave exposure preference as "protected."

Life History. Little information is available on the life history of *A. jacquelineae*. Generally, *Acropora* species have rapid skeletal growth and low tolerance to stress, and all are hermaphroditic broadcast spawners (Brainard et al. 2011). As noted in the *A. globiceps* life history section above, all 37 *Acropora* species (which did not include *A. jacquelineae*) in Darling et al.'s (2012) global coral life history study were classified as "competitive species," based on broadcast spawning, rapid skeletal growth, and branching colony morphology. These life history characteristics allow *Acropora* species to recruit quickly to available substrate and successfully compete for space, but also make them susceptible to disturbance, thus they typically are only dominant in ideal conditions (Darling et al. 2012). Whether *A. jacquelineae*'s reproductive life history differs from that of shallow *Acropora* species, as has been found for the mesophotic species *A. tenella* (see Section 3.8 below), is unknown.

4.2.2. Distribution

Geographic Distribution. *Acropora jacquelineae* has a relatively limited geographic distribution occurring in 15 MEOWs (Fig. 8) and does not occur in U.S. waters, based on information in NMFS (2022c). Its distribution is limited mainly to the Coral Triangle region in the western equatorial Pacific Ocean, which is projected to have the most rapid and severe impacts from climate change and localized human impacts for coral reefs over the 21st century. The current information indicates that *A. jacquelineae* occurs in two more MEOWs than we were aware of at the time of listing in 2014, both of which are outside the Coral Triangle in the western Pacific (Micronesia, New Caledonia; NMFS 2022c). Occurrence throughout the Coral Triangle and in multiple archipelagos in the western Pacific indicates that the species' geographic distribution is considerably larger than previously known.

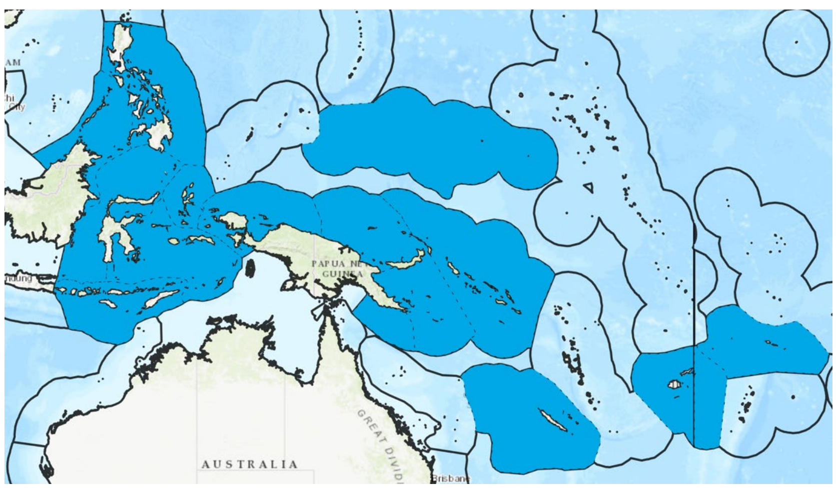


Figure 8. Geographic distribution of *A. jacquelineae*.

Depth Distribution. *Acropora jacquelineae* is found on walls and ledges from approximately 10 m (Wallace and Wolstenholme 1998) to 50 m of depth (Turak and DeVantier 2019). Thus, current information indicates that *A. jacquelineae* has a larger depth range (10–50 m) than we were aware of at the time of listing in 2014 (10–35 m).

Relevance of Distribution to Status. Geographic and depth distributions were the key spatial factors considered in determining the status of coral species and in the listing of *A. jacquelineae* in 2014. A narrow geographic or depth distribution exacerbates a species' extinction risk because larger proportions of the population are likely to be exposed to any single disturbance. In contrast, a broad overall distribution moderates a species' extinction risk because the population is distributed across a range of geographic areas and depths, and thus lower proportions of the populations are likely to be exposed to any single disturbance. For example, one reason that *A. jacquelineae* was listed was because the information available at that time indicated a narrow geographic distribution limited to the Coral Triangle (79 FR 53851). Since both the geographic and depth distributions of *A. jacquelineae* are greater than we were aware of at the time of listing in 2014, its distribution has a greater capacity to moderate extinction risk.

4.2.3. Abundance

Relative Abundance: DeVantier and Turak (2017) characterized abundances of over 600 Indo-Pacific reef-building coral species in 31 Veron ecoregions from the Red Sea to Fiji, as further described in Section 4.1.3 above. *Acropora jacquelineae* was recorded in 8 of the 31 ecoregions. Within those 8 ecoregions, it had a mean overall abundance of 8.97 (Uncommon), ranging from 0.40 (Rare) in the Lesser Sunda Islands and Savu Sea Ecoregion to 25.76 (Common) in the Cenderawasih Bay, Papua Ecoregion. The mean overall abundance of *A. jacquelineae* for all 31 ecoregions was 2.28 (Uncommon, DeVantier and Turak 2017, Table S2), however some of the 23 ecoregions where it was not recorded may be outside its range. The Coral Traits Database (https://coraltraits.org/, accessed August 2022) lists *A. jacquelineae*'s global relative abundance as "uncommon," but does not cite DeVantier and Turak (2017). Within its range, the relative abundance of *A. jacquelineae* may vary locally from very rare to at least common. However, based on the above information, the rangewide relative abundance of *A. jacquelineae* is uncommon.

Absolute Abundance. Based on information from Richards et al. (2008, 2019), *A. jacquelineae* had a population estimate of 31,599,000 colonies, and an effective population size of 3,476,000 colonies (79 FR 53851). However, *A. jacquelineae*'s distribution is larger than assumed by Richards et al. (2008, 2019). Based on the updated information, *A. jacquelineae*'s absolute abundance is likely to be at least tens of millions of colonies, which similar to what was known in 2014.

Abundance Trends. As described above in the general Threats Evaluation and below for threats to *A. jacquelineae*, the most important threats (i.e., ocean warming, ocean acidification) have worsened since 2014, and substantial impacts to *Acropora* species have occurred, although no species-specific data are available for *A. jacquelineae*. Based on the continued worsening in the most important threats, it is likely that *A. jacquelineae* is decreasing in overall abundance (i.e., abundance across all the ecoregions that make up its range).

Relevance of Abundance to Status. Abundance is the key demographic factor considered in determining the status of coral species and in the listing of *A. jacquelineae* in 2014. A low relative or absolute abundance, especially in combination with declining abundance, exacerbates a species' extinction risk because larger proportions of the population are likely to be exposed to any single disturbance. In contast, a higher relative or absolute abundance moderates a species' extinction risk because lower proportions of the population are likely to be exposed to any single disturbance (79 FR 53851).

4.2.4. Threats

This section provides an updated threats evaluation for *A. jacquelineae*, focusing on the threats that contributed to its listing (79 FR 53851), including ocean warming, ocean acidification, disease, fishing, LBSP, predation, and inadequacy of existing regulatory mechanisms. In addition, current information indicates that collection and trade is also impacting the status of the species. A threats summary table is provided, including relative importance ratings for the threats, effects of threats since listing in 2014, and projected effects of threats in the foreseeable future.

Ocean Warming: As noted in Section 3.2.1 above, since listing in 2014, the effects of ocean warming on Indo-Pacific reef-building corals have substantially worsened. In response to the 2014–2017 series of warming-induced bleaching events, *Acropora* corals were generally the most impacted coral taxa in different locations around the Indo-Pacific (e.g., Hoogenboom et al. 2017, Frade et al 2018, Hughes et al. 2018a,b, Raymundo et al. 2019, Thinesh et al. 2019, Dietzel et al. 2020, Gilmour et al. 2022). Section 3.2.1 also describes how ocean warming is projected to greatly worsen in the foreseeable future (i.e., between now and 2100). In conclusion, the current information indicates that *A. jacquelineae* continues to be highly susceptible to ocean warming, that this threat has substantially worsened since listing in 2014, and that it will greatly worsen in the foreseeable future (Table 5).

Ocean Acidification: As noted in Section 3.2.2 above, since listing in 2014, the effects of ocean acidification on Indo-Pacific reef-building corals have worsened. Generally, *Acropora* species are susceptible to reduced calcification and skeletal growth from ocean acidification (Brainard et al. 2011, 79 FR 53851, Smith et al. 2020, Evenson et al. 2021, Hill and Hoogenboom 2022). Section 3.2.2 also describes how ocean acidification is projected to greatly worsen in the foreseeable future. In conclusion, the current information indicates that *A. jacquelineae* continues to be susceptible to ocean acidification, that this threat has worsened since listing in 2014, and that it will greatly worsen in the foreseeable future (Table 5).

Disease: As noted in Section 3.2.3 above, since listing in 2014, the effects of disease on Indo-Pacific corals have increased, mainly in response to the 2014–2017 bleaching events. Generally, *Acropora* species are susceptible to most of the diseases that infect coral, and are more commonly affected by acute and lethal diseases than other corals (Brainard et al. 2011, 79 FR 53851, Hobbs et al. 2015, Aeby et al. 2020, Howells et al. 2020). Section 3.2.3 also describes how disease is projected to substantially worsen in the foreseeable future. In conclusion, the current information indicates that *A. jacquelineae* continues to be susceptible to disease, that this threat has worsened since listing in 2014, and that it will substantially worsen in the foreseeable future (Table 5).

Fishing: As noted in Section 3.2.4 above, since listing in 2014, the direct and indirect effects of fishing on Indo-Pacific corals have continued, likely intensifying in some locations while lessening in others due to various factors. Generally, branching, fast-growing corals such as most *Acropora* species are susceptible to direct (i.e., damage by fishing gear because of their morphology) and indirect (i.e., increased competition for space with algae) effects of fishing (Brainard et al. 2011, 79 FR 53851). Section 3.2.4 also describes how fishing is projected to substantially worsen in the foreseeable future. In conclusion, the current information indicates that *A. jacquelineae* continues to be susceptible to fishing, that this threat has continued since listing in 2014, and that it will substantially worsen in the foreseeable future (Table 5).

LBSP: As noted in Section 3.2.5 above, since listing in 2014, the effects of LBSP on Indo-Pacific corals have continued, likely intensifying in some locations while lessening in others due to various factors. Generally, *Acropora* species are relatively susceptible to sediment and nutrients compared to other reef-building coral taxa (Brainard et al. 2011, 79 FR 53851, Carlson et al. 2019, Tuttle and Donahue 2022). Section 3.2.5 also describes how LBSP is projected to substantially worsen in the foreseeable future. In conclusion, the current information indicates that *A. jacquelineae* continues to be susceptible to LBSP, that this threat has continued since listing in 2014, and that it will substantially worsen in the foreseeable future (Table 5).

Predation: As noted in Section 3.2.6 above, since listing in 2014, the effects of predation on Indo-Pacific corals have increased, mainly because the 2014–2017 bleaching events resulted in more favorable conditions for predators such as COTS. Generally, *Acropora* species are relatively susceptible to predation compared to other reef-building coral taxa (Brainard et al. 2011, 79 FR 53851, Keesing et al. 2019, Tkachenko and Huang 2022). Section 3.2.6 also describes how predation is projected to substantially worsen in the foreseeable future. In conclusion, the current information indicates that *A. jacquelineae* continues to be susceptible to predation, that this threat has worsened since listing in 2014, and that it will substantially worsen in the foreseeable future (Table 5).

Collection and Trade: Although collection and trade did not contributed to the listing of *A. globiceps* (79 FR 53851), the following information indicates that this threat is likely impacting the status of the species. As noted in Section 3.2.7 above, since listing in 2014, the effects of collection and trade on Indo-Pacific corals have continued. Generally, *Acropora* species are relatively susceptible to collection and trade compared to other reef-building coral taxa (Brainard et al. 2011, 79 FR 53851). According to the CITES database cited in Section 3.2.7, between 1985 and 2017, over 17 million *Acropora* units were globally imported and exported. These units were not identified to species, thus likely included an undeterminable number of unidentified *A. jacquelineae*. In addition, the database also records that between 2009 and 2017, hundreds to thousands of *A. jacquelineae* units were globally imported and exported annually (NMFS 2022a). Because of the popularity of *A. jacquelineae* in the marine aquarium trade (Adams 2016) as well as the ongoing and projected growth in the industry, collection and trade may increasingly impact the status of *A. jacquelineae*. Section 3.2.7 also describes how collection and trade is projected to substantially worsen in the foreseeable future. In conclusion, the current information indicates that *A. jacquelineae* is susceptible to collection and trade, that this threat has continued since listing in 2014, and that it will substantially worsen in the foreseeable future (Table 5).

Sea-level Rise: As noted in Section 3.2.8 above, since listing in 2014, sea-level rise has likely been too gradual to result in measurable effects on Indo-Pacific reef-building corals. In those cases where earthquakes have resulted in substrate uplift resembling sea-level rise, these substrates have been colonized by rapidly-growing corals like *Acropora* species. In conclusion, as in the final rule, the current information indicates that *A. jacquelineae* is not susceptible to sea-level rise, that there have been no detectable trends in the effects of this threat since listing in 2014, but that it will worsen in the foreseeable future (Table 5).

Regulatory Mechanisms: As noted in Section 3.2.9 above, since listing in 2014, some progress has been made with GHG management as well as controlling local threats, although existing regulatory mechanisms are still inadequate to control any of the threats. Section 3.2.9 also describes how it is unlikely that regulatory mechanisms will be improved to the point where they are adequate to control any of the threats in the foreseeable future. In conclusion, the current information indicates that existing regulatory mechanisms remain inadequate to control any threat to *A. jacquelineae*, and that improvement is unlikely in the foreseeable future (Table 5).

Threats Conclusion for *A. jacquelineae*: Since *A. jacquelineae* was listed in 2014, many of the threats to the species have worsened. Especially concerning is that the most important threat to the species, ocean warming, has substantially worsened. In addition, all threats are projected to worsen in the foreseeable future, with the possible exception of regulatory mechanisms, which may continue to improve but also are likely to remain inadequate for controlling any of the threats (Table 5).

Although the final rule rated the relative importance of threats to the world's reef-building corals (Table 2), it did not apply those ratings to *A. jacquelineae* (79 FR 53851). Instead, the final rule concluded that *A. jacquelineae* is highly susceptible to ocean warming and susceptible to ocean acidification, disease, fishing, LBSP, and predation, while regulatory mechanisms were inadequate for controlling any threat (79 FR 53851). However, as summarized above, we now have more genus-specific and species-specific information available on the importance of each threat to *Acropora* species and *A. jacquelineae*, respectively. Based on the general importance ratings of the threats to Indo-Pacific reef-building corals (Table 3) and the genus-specific and species-specific information above, we conclude that the relative importance ratings of each threat to Indo-Pacific corals apply to *A. jacquelineae*. In addition, the observed threat trends since 2014 and projected threat trends in the foreseeable future are provided (Table 5).

Table 5. Summary of threats evaluation for *A. jacquelineae*. For each threat, relative importance to the extinction risk of the species, observed trend since 2014, and projected trend in the foreseeable future are provided.

Threat (listing factor)	**Importance**	**Observed Trend in Effects Since 2014**	**Projected Trend in Effects to 2100**
Ocean Warming (Factor E)	Very High	Substantially worsened	Greatly worsen
Ocean Acidification (Factor E)	High	Worsened	Greatly worsen
Disease (Factor C)	High	Worsened	Substantially worsen
Fishing (Factor A)	Medium	Continued	Substantially worsen
LBSP (Factors A and E)	Low-Medium	Continued	Substantially worsen
Predation (Factor C)	Low-Medium	Worsened	Substantially worsen
Collection and Trade (Factor B)	Low-Medium	Continued	Substantially worsen
Sea-level Rise (Factor E)	Low	No detectable trends	Worsen
Inadequacy of Existing Regulatory Mechanisms (Factor D)	High	Some improvement but still inadequate	Improvement but likely still inadequate

4.2.5. Conclusion

As explained in the 2014 final listing rule (79 FR 53851), a species' vulnerability to extinction results from the combination of its spatial (i.e., distribution) and demographic (i.e., abundance) characteristics, threat susceptibilities, and consideration of the baseline environment and future projections of threats. *Acropora jacquelineae* was listed as threatened in 2014 because of its limited geographic distribution restricted to the Coral Triangle and western Pacific, low abundance, high susceptibility to ocean warming, susceptibilities to ocean acidification, disease, fishing, LBSP, predation, inadequate regulatory mechanisms, declining baseline conditions, and projected worsening of threats (79 FR 53851).

Since 2014, we have learned that *A. jacquelineae* has: (1) a broader geographic distribution (15 MEOWs instead of 13); and (2) a broader depth distribution (10–50 m instead of 10–35 m). That is, *A. jacquelineae* is more broadly distributed than we believed in 2014, and thus may have a higher capacity to moderate the effects of the threats, as explained in the Relevance of Distribution to Status section above.

Since 2014, the effects of ocean warming have substantially worsened, and the effects of most other threats have worsened as well. All threats are projected to substantially worsen under current global GHG regulatory mechanisms, which would result in global warming of 2.6–3.4°C above the pre-industrial baseline by 2100 (see Fig. 4 in Section 3.1 above). Even if the goal of the Paris Agreement is achieved (i.e., limiting global warming to 1.5°C above pre-industrial by 2100), the threats would become much worse than they are currently (Dixon et al. 2022), likely preventing the recovery of *A. jacquelineae*. Current regulatory mechanisms are grossly inadequate, especially GHG management.

In conclusion, the above information shows that *A. jacquelineae* is more broadly distributed than we believed in 2014, but that the threats have worsened and that collection and trade is also an important threat to the species. Especially concerning is that the most important threat to the species, ocean warming, has substantially worsened since the species was listed in 2014. The other important threats to the species, including ocean acidification, disease, fishing, LBSP, predation, and collection and trade have also either worsened or continued since 2014. While there has been some progress with regulatory mechanisms, primarily because of the 2016 Paris Agreement, regulatory mechanisms for both global and local threats are still inadequate. However, the species' distribution is broader than we were aware of at the time of listing in 2014, which is a key factor for moderating threats.

4.3. *Acropora lokani* (Wallace 1994)

4.3.1. Biology

Taxonomy. *Acropora lokani* was described by Wallace (1994), with additional taxonomic details provided in more recent publications (Wallace 1999, Wallace et al. 2012). It is included in the Corals of the World books (Veron 2000) and website (http://www.coralsoftheworld.org/, accessed August 2022), and is accepted by WoRMS (Hoeksma and Cairns 2021).

Morphology. Colonies are flat-topped and usually of moderate size. Larger branches spread horizontally and have short, upward growing small branchlets. Long tubular corallites extend upwards at various angles from the branchlets (Fig. 9). The species is similar to *A. caroliniana*, except that the axial corallites of *A. caroliniana* radiate in a Christmas tree-like formation, tapering along their length. Colonies are cream, brown, or blue in color (Veron 2000, 2016).

Figure 9. *Acropora lokani*, showing colony and branch morphology. Colony photo from Fiji (Emre Turak), branch photo from the Philippines (Charlie Veron; Veron et al. 2016).

Habitat. *Acropora lokani* occurs in sheltered lagoonal patch reefs (Wallace 1994) and a range of other reef habitats (Veron et al. 2016, Chalias 2019a,b). The Coral Traits Database (https://coraltraits.org/, accessed August 2022) lists *A. lokani*'s water clarity preference as "clear," and wave exposure preference as "broad."

Life History. Little information is available on the life history of *A. lokani*. Generally, *Acropora* species have rapid skeletal growth and low tolerance to stress, and all are hermaphroditic broadcast spawners (Brainard et al. 2011). As noted in the *A. globiceps* life history section above, all 37 *Acropora* species (which did not include A. *lokani*) in Darling et al.'s (2012) global coral life history study were classified as "competitive species," based on broadcast spawning, rapid skeletal growth, and branching colony morphology. These life history characteristics allow *Acropora* species to recruit quickly to available substrate and successfully compete for space, but also make them susceptible to disturbance, thus they typically are only dominant in ideal conditions (Darling et al. 2012).

4.3.2. Distribution

<u>Geographic Distribution</u>. *Acropora lokani* has a relatively limited distribution, occurring in 14 MEOWs (Fig. 10) and does not occur in U.S. waters, based on information in NMFS (2022c). Its distribution is largely restricted to the Coral Triangle and the western equatorial Pacific Ocean, which is projected to have the most rapid and severe impacts from climate change and localized human impacts for coral reefs over the 21st century. The current information indicates that *A. lokani* occurs in one more Veron ecoregion (Sunda Shelf between Malaysia and Borneo) than we were aware of 2014 (i.e., 21 Veron ecoregions instead of 20). However, because Veron ecoregions are smaller than MEOWs (see Section 2.2), the species still occurs in the same number of MEOWs as we were aware of in 2014 (i.e., 14 MEOWs, NMFS 2022c).

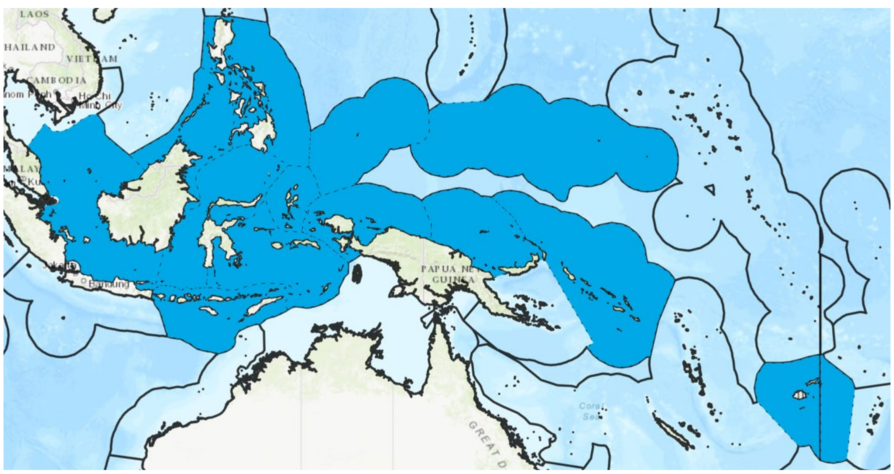


Figure 10. Geographic distribution of *A. lokani*.

<u>Depth Distribution</u>. The shallowest that *A. lokani* has been reported from varies from 8 m (Carpenter et al. 2008) to 12–15 m (Chalias 2019a,b), and the deepest from 40 m (Muir and Pichon 2019) to >50 m (Chalias 2019a), giving a depth distribution of approximately 8 – 50 m. Thus, current information indicates that *A. lokani* has a larger depth range (8–50 m) than we were aware of at the time of listing in 2014 (8–25 m).

<u>Relevance of Distribution to Status</u>. Geographic and depth distributions were the key spatial factors considered in determining the status of coral species and in the listing of *A. lokani* in 2014. A narrow geographic or depth distribution exacerbates a species' extinction risk because larger proportions of the population are likely to be exposed to any single disturbance. In contrast, a broad overall distribution moderates a species' extinction risk because the population is distributed across a range of geographic areas and depths, and thus lower proportions of the populations are likely to be exposed to any single disturbance. For example, one reason that *A. lokani* was listed was because the information available at that time indicated a small geographic distribution (79 FR 53851). Since both the geographic and depth distributions of *A. lokani* are greater than we were aware of at the time of listing in 2014, its distribution has a greater capacity to moderate extinction risk.

4.3.3. Abundance

Relative Abundance: DeVantier and Turak (2017) characterized abundances of over 600 Indo-Pacific reef-building coral species in 31 Veron ecoregions from the Red Sea to Fiji, as further described in Section 4.1.3 above. *Acropora lokani* was recorded in 14 of the 31 ecoregions. Within those 14 ecoregions, it had a mean overall abundance of 9.17 (Uncommon), ranging from 0.17 (Rare) in the Great Barrier Reef North-central Ecoregion to 28.26 (Common) in the Fiji Ecoregion. The mean overall abundance of *A. lokani* for all 31 ecoregions was 3.87 (Uncommon, DeVantier and Turak 2017, Table S2), however some of the 17 ecoregions where it was not recorded may be outside its range. The Coral Traits Database (https://coraltraits.org/, accessed August 2022) lists *A. lokani*'s global relative abundance as "uncommon," but does not cite DeVantier and Turak (2017). Within its range, the relative abundance of *A. lokani* may vary locally from very rare to at least common. However, based on the above information, the rangewide relative abundance of *A. lokani* is uncommon.

Absolute Abundance. Based on information from Richards et al. (2008, 2019), *A. lokani* had a population estimate of 18,960,000 colonies, and an effective population size of 2,086,000 colonies (79 FR 53851). However, *A. lokani*'s distribution is larger than assumed by Richards et al. (2008, 2019). Based on the updated information, *A. lokani*'s absolute abundance is likely to be at least tens of millions of colonies, which similar to what was known in 2014.

Abundance Trends. As described above in the general Threats Evaluation and below for threats to *A. lokani*, the most important threats (i.e., ocean warming, ocean acidification) have worsened since 2014, and substantial impacts to *Acropora* species have occurred, although no species-specific data are available for *A. lokani*. Based on the continued worsening of the most important threats, it is likely that *A. lokani* is decreasing in overall abundance (i.e., abundance across all the ecoregions that make up its range).

Relevance of Abundance to Status. Abundance is the key demographic factor considered in determining the status of coral species and in the listing of *A. lokani* in 2014. A low relative or absolute abundance, especially in combination with declining abundance, exacerbates a species' extinction risk because larger proportions of the population are likely to be exposed to any single disturbance. In contrast, a higher relative or absolute abundance moderates a species' extinction risk because lower proportions of the population are likely to be exposed to any single disturbance (79 FR 53851).

4.3.4. Threats

This section provides an updated threats evaluation for *A. lokani*, focusing on the threats that contributed to its listing (79 FR 53851), including ocean warming, ocean acidification, disease, fishing, LBSP, predation, and inadequacy of existing regulatory mechanisms. In addition, current information indicates that collection and trade is also impacting the status of the species. A threats summary table is provided, including relative importance ratings for the threats, effects of threats since listing in 2014, and projected effects of threats in the foreseeable future.

Ocean Warming: As noted in Section 3.2.1 above, since listing in 2014, the effects of ocean warming on Indo-Pacific reef-building corals have substantially worsened. In response to the 2014–2017 series of warming-induced bleaching events, *Acropora* corals were generally the most impacted coral taxa in different locations around the Indo-Pacific (e.g., Hoogenboom et al. 2017, Frade et al 2018, Hughes et al. 2018a,b, Raymundo et al. 2019, Thinesh et al. 2019, Dietzel et al. 2020, Gilmour et al. 2022). Section 3.2.1 also describes how ocean warming is projected to greatly worsen in the foreseeable future (i.e., between now and 2100). In conclusion, the current information indicates that *A. lokani* continues to be highly susceptible to ocean warming, that this threat has substantially worsened since listing in 2014, and that it will greatly worsen in the foreseeable future (Table 6).

Ocean Acidification: As noted in Section 3.2.2 above, since listing in 2014, the effects of ocean acidification on Indo-Pacific reef-building corals have worsened. Generally, *Acropora* species are susceptible to reduced calcification and skeletal growth from ocean acidification (Brainard et al. 2011, 79 FR 53851, Smith et al. 2020, Evenson et al. 2021, Hill and Hoogenboom 2022). Section 3.2.2 also describes how ocean acidification is projected to greatly worsen in the foreseeable future. In conclusion, the current information indicates that *A. lokani* continues to be susceptible to ocean acidification, that this threat has worsened since listing in 2014, and that it will greatly worsen in the foreseeable future (Table 6).

Disease: As noted in Section 3.2.3 above, since listing in 2014, the effects of disease on Indo-Pacific corals have increased, mainly in response to the 2014 – 2017 bleaching events. Generally, *Acropora* species are susceptible to most of the diseases that infect coral, and are more commonly affected by acute and lethal diseases than other corals (Brainard et al. 2011, 79 FR 53851, Hobbs et al. 2015, Aeby et al. 2020, Howells et al. 2020). Section 3.2.3 also describes how disease is projected to substantially worsen in the foreseeable future. In conclusion, the current information indicates that *A. lokani* continues to be susceptible to disease, that this threat has worsened since listing in 2014, and that it will substantially worsen in the foreseeable future (Table 6).

Fishing: As noted in Section 3.2.4 above, since listing in 2014, the direct and indirect effects of fishing on Indo-Pacific corals have continued, likely intensifying in some locations while lessening in others due to various factors. Generally, branching, fast-growing corals such as most *Acropora* species are susceptible to direct (i.e., damage by fishing gear because of their morphology) and indirect (i.e., increased competition for space with algae) effects of fishing (Brainard et al. 2011, 79 FR 53851). Section 3.2.4 also describes how fishing is projected to substantially worsen in the foreseeable future. In conclusion, the current information indicates that *A. lokani* continues to be susceptible to fishing, that this threat has continued since listing in 2014, and that it will substantially worsen in the foreseeable future (Table 6).

LBSP: As noted in Section 3.2.5 above, since listing in 2014, the effects of LBSP on Indo-Pacific corals have continued, likely intensifying in some locations while lessening in others due to various factors. Generally, *Acropora* species are relatively susceptible to sediment and nutrients compared to other reef-building coral taxa (Brainard et al. 2011, 79 FR 53851, Carlson et al. 2019, Tuttle and Donahue 2022). Section 3.2.5 also describes how LBSP is projected to substantially worsen in the foreseeable future. In conclusion, the current information indicates that *A. lokani* continues to be susceptible to LBSP, that this threat has continued since listing in 2014, and that it will substantially worsen in the foreseeable future (Table 6).

Predation: As noted in Section 3.2.6 above, since listing in 2014, the effects of predation on Indo-Pacific corals have increased, mainly because the 2014 – 2017 bleaching events resulted in more favorable conditions for predators such as COTS. Generally, *Acropora* species are relatively susceptible to predation compared to other reef-building coral taxa (Brainard et al. 2011, 79 FR 53851, Keesing et al. 2019, Tkachenko and Huang 2022). Section 3.2.6 also describes how predation is projected to substantially worsen in the foreseeable future. In conclusion, the current information indicates that *A. lokani* continues to be susceptible to predation, that this threat has worsened since listing in 2014, and that it will substantially worsen in the foreseeable future (Table 6).

Collection and Trade: Although collection and trade did not contribute to the listing of *A. lokani* (79 FR 53851), the following information indicates that this threat is likely impacting the status of the species. As noted in Section 3.2.7 above, since listing in 2014, the effects of collection and trade on

Indo-Pacific corals have continued. Generally, *Acropora* species are relatively susceptible to collection and trade compared to other reef-building coral taxa (Brainard et al. 2011, 79 FR 53851). According to the CITES database cited in Section 3.2.7, between 1985 and 2017, over 17 million *Acropora* units were globally imported and exported. These units were not identified to species, thus likely included an undeterminable number of unidentified *A. lokani*. In addition, the database also records that between 2003 and 2017, dozens to hundreds of *A. lokani* units were globally imported and exported annually (NMFS 2022a). Because of the popularity of *A. lokani* in the marine aquarium trade (Chalias 2019a,b) as well as the ongoing and projected growth in the industry, collection and trade may increasingly impact the status of *A. lokani*. Section 3.2.7 also describes how collection and trade is projected to substantially worsen in the foreseeable future. In conclusion, the current information indicates that *A. lokani* is susceptible to collection and trade, that this threat has continued since listing in 2014, and that it will substantially worsen in the foreseeable future (Table 6).

<u>Sea-level Rise</u>: As noted in Section 3.2.8 above, since listing in 2014, sea-level rise has likely been too gradual to result in measurable effects on Indo-Pacific reef-building corals. In those cases where earthquakes have resulted in substrate uplift resembling sea-level rise, these substrates have been colonized by rapidly-growing corals like *Acropora* species. In conclusion, as in the final rule, the current information indicates that *A. lokani* is not susceptible to sea-level rise, that there have been no detectable trends in the effects of this threat since listing in 2014, but that it will worsen in the foreseeable future (Table 6).

<u>Regulatory Mechanisms</u>: As noted in Section 3.2.9 above, since listing in 2014, some progress has been made with GHG management as well as controlling local threats although existing regulatory mechanisms are still inadequate to control any of the threats. Section 3.2.9 also describes how it is unlikely that regulatory mechanisms will be improved to the point where they are adequate to control any of the threats in the foreseeable future. In conclusion, the current information indicates that existing regulatory mechanisms remain inadequate to control any threat to *A. lokani*, and that improvement is unlikely in the foreseeable future (Table 6).

<u>Threats Conclusion for *A. lokani*</u>: Since *A. lokani* was listed in 2014, many of the threats to the species have worsened. Especially concerning is that the most important threat to the species, ocean warming, has substantially worsened. In addition, all threats are projected to worsen in the foreseeable future, with the possible exception of regulatory mechanisms, which may continue to improve but also are likely to remain inadequate for controlling any of the threats (Table 6).

Although the final rule rated the relative importance of threats to the world's reef-building corals (Table 2), it did not apply those ratings to *A. lokani* (79 FR 53851). Instead, the final rule concluded that *A. lokani* is highly susceptible to ocean warming and susceptible to ocean acidification, disease, fishing, LBSP, and predation, while regulatory mechanisms were inadequate for controlling any threat (79 FR 53851). However, as summarized above, we now have more genus-specific and species-specific information available on the importance of each threat to *Acropora* species and *A. lokani*, respectively. Based on the general importance ratings of the threats to Indo-Pacific reef-building corals (Table 3) and the genus-specific and species-specific information above, we conclude that the relative importance ratings of each threat to Indo-Pacific corals apply to *A. lokani*. In addition, the observed threat trends since 2014 and projected threat trends in the foreseeable future are provided (Table 6).

Table 6. Summary of threats evaluation for *A. lokani*. For each threat, relative importance to the extinction risk of the species, observed trend since 2014, and projected trend in the foreseeable future are provided.

Threat (listing factor)	Importance	Observed Trend in Effects Since 2014	Projected Trend in Effects to 2100
Ocean Warming (Factor E)	Very High	Substantially worsened	Greatly worsen
Ocean Acidification (Factor E)	High	Worsened	Greatly worsen
Disease (Factor C)	High	Worsened	Substantially worsen
Fishing (Factor A)	Medium	Continued	Substantially worsen
LBSP (Factors A and E)	Low-Medium	Continued	Substantially worsen
Predation (Factor C)	Low-Medium	Worsened	Substantially worsen
Collection and Trade (Factor B)	Low-Medium	Continued	Substantially worsen
Sea-level Rise (Factor E)	Low	No detectable trends	Worsen
Inadequacy of Existing Regulatory Mechanisms (Factor D)	High	Some improvement but still inadequate	Improvement but likely still inadequate

4.3.5. Conclusion

As explained in the 2014 final listing rule (79 FR 53851), a species' vulnerability to extinction results from the combination of its spatial (i.e., distribution) and demographic (i.e., abundance) characteristics, threat susceptibilities, and consideration of the baseline environment and future projections of threats. *Acropora lokani* was listed as threatened in 2014 because of its limited geographic distribution largely restricted to the Coral Triangle region and parts of the western equatorial Pacific Ocean, low abundance, high susceptibility to ocean warming, susceptibilities to ocean acidification, fishing, LBSP, disease, and predation, inadequate regulatory mechanisms, declining baseline conditions, and projected worsening of threats (79 FR 53851).

Since 2014, we have learned that *A. lokani* has a larger geographic distribution (21 instead of 20 Veron ecoregions) and broader depth distribution (8–50 m instead of 8–25 m) than we believed in 2014. That is, *A. lokani* is more broadly distributed than we believed in 2014, and thus may have a higher capacity to moderate the effects of the threats, as explained in the Relevance of Distribution to Status section above.

Since 2014, the effects of ocean warming have substantially worsened, and the effects of most other threats have worsened as well. All threats are projected to substantially worsen under current global GHG regulatory mechanisms, which would result in global warming of 2.6–3.4°C above the pre-industrial baseline by 2100 (see Fig. 4 in Section 3.1 above). Even if the goal of the Paris Agreement is achieved (i.e., limiting global warming to 1.5°C above pre-industrial by 2100), the threats would become much worse than they are currently (Dixon et al. 2022), likely preventing the recovery of *A. lokani*. Current regulatory mechanisms are grossly inadequate, especially GHG management.

In conclusion, the above information shows that *A. lokani* is more broadly distributed than we believed in 2014, but that the threats have worsened and that collection and trade is also an important threat to the species. Especially concerning is that the most important threat to the species, ocean warming, has substantially worsened since the species was listed in 2014. The other important threats to the species, including ocean acidification, disease, fishing, LBSP, predation, and collection and trade have also either worsened or continued since 2014. While there has been some progress with regulatory mechanisms, primarily because of the 2016 Paris Agreement, regulatory mechanisms for both global and local threats are still inadequate. However, the species' distribution is broader than we were aware of at the time of listing in 2014, which is a key factor for moderating threats.

4.4. *Acropora pharaonis* (Milne Edwards 1860)

4.4.1. Biology

Taxonomy. This species was originally described as *Madrepora pharaonis* (Milne Edwards 1860), then assigned to the genus *Acropora* (Verrill 1902). Additional taxonomic details are provided in Wallace (1999) and Wallace et al. (2012). It is included in the Corals of the World books (Veron 2000) and website (http://www.coralsoftheworld.org/, accessed August 2022), and is accepted by WoRMS (Hoeksma and Cairns 2021).

Morphology. Colonies are large horizontal tables or irregular clusters of horizontal or upright interlinked contorted branches up to two meters in diameter (Wallace 1999). Branches are pointed and have short branchlets that link main branches. Colonies are grey-brown in color, usually with pale branch tips (Fig. 11, Veron et al. 2016).

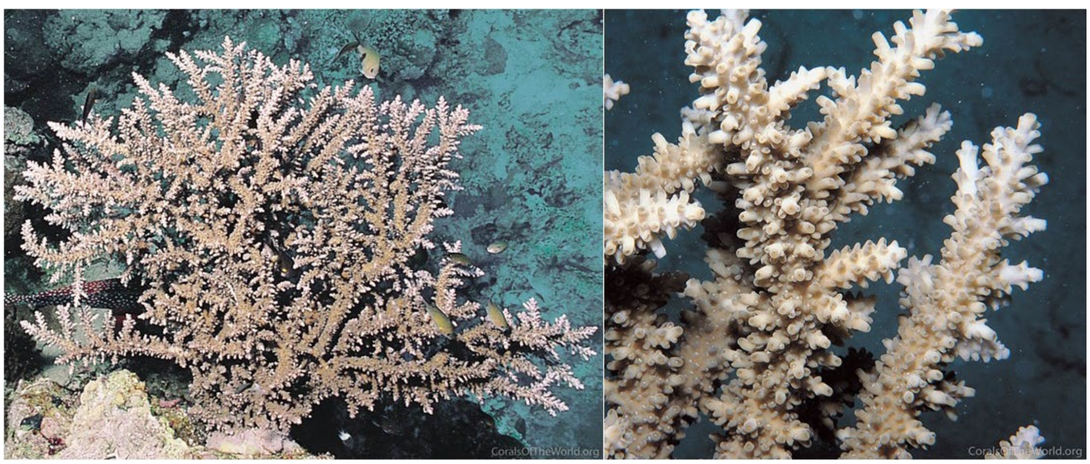


Figure 11. *Acropora pharaonis*, showing colony (Red Sea, Charlie Veron) and branch (Madagascar, Charlie Veron) morphology (Veron et al. 2016).

Habitat. *Acropora pharaonis* occurs in sheltered habitats such as lagoons and deep reef slopes (Veron et al. 2016). The Coral Traits Database (https://coraltraits.org/, accessed August 2022) lists *A. pharaonis*'s water clarity preference as "clear," and wave exposure preference as "protected."

Life History. Little information is available on the life history of *A. pharaonis*. Generally, *Acropora* species have rapid skeletal growth and low tolerance to stress, and all are hermaphroditic broadcast spawners (Brainard et al. 2011). As noted in the *A. globiceps* life history section above, all 37 *Acropora* species (which did not include A. *pharaonis*) in Darling et al.'s (2012) global coral life history study were classified as "competitive species," based on broadcast spawning, rapid skeletal growth, and branching colony morphology. These life history characteristics allow *Acropora* species to recruit quickly to available substrate and successfully compete for space, but also make them susceptible to disturbance, thus they typically are only dominant in ideal conditions (Darling et al. 2012).

4.4.2. Distribution

Geographic Distribution. *Acropora pharaonis* has a relatively limited distribution, occurring in 19 MEOWs (Fig. 12) and does not occur in U.S. waters, based on information in NMFS (2022c). Its distribution includes the Red Sea and Arabian Gulf, but relatively few islands, and includes areas projected to have the most rapid and severe impacts from climate change and localized human impacts for coral reefs over the 21st century (*i.e.,* the Red Sea and the Arabian Gulf). The current information indicates that *A. pharaonis* occurs in one more Veron ecoregion (Gulf of Oman) than we were aware of 2014 (i.e., 20 Veron ecoregions instead of 19). However, because Veron ecoregions are smaller than MEOWs (see Section 2.2), the species still occurs in the same number of MEOWs as we were aware of in 2014 (i.e., 19 MEOWs, NMFS 2022c).

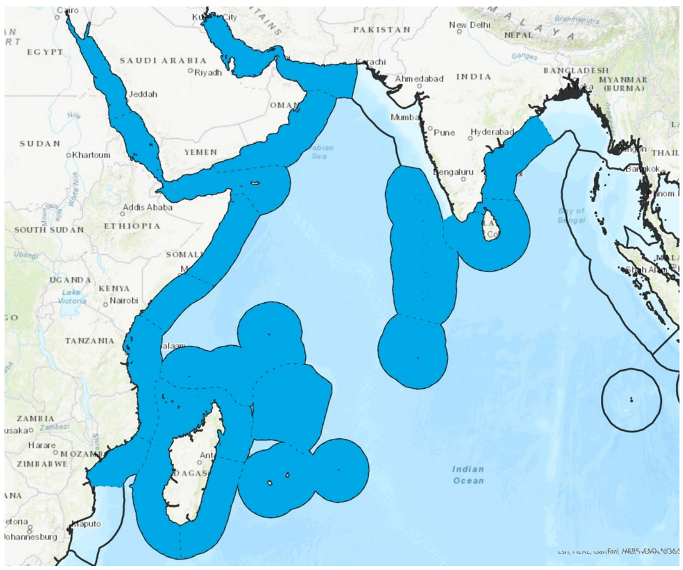


Figure 12. Geographic distribution of *A. pharaonis*.

Depth Distribution. *Acropora pharaonis* has been reported from 2 m (Coral Traits Database https://coraltraits.org/, accessed August 2022) to 44 m of depth (Kahng et al. 2019). Thus, current information indicates that *A. pharaonis* has a broader depth range (2–44 m) than we were aware of at the time of listing in 2014 (5–25 m).

Relevance of Distribution to Status. Geographic and depth distributions were the key spatial factors considered in determining the status of coral species and in the listing of *A. pharaonis* in 2014. A narrow geographic or depth distribution exacerbates a species' extinction risk because larger proportions of the population are likely to be exposed to any single disturbance. In contrast, a broad overall distribution moderates a species' extinction risk because the population is distributed across a range of geographic areas and depths, and thus lower proportions of the populations are likely to be exposed to any single disturbance. For example, one reason that *A. pharaonis* was listed was because of its limited geographic distribution (79 FR 53851). Since both the geographic and depth distributions of *A. pharaonis* are greater than we were aware of at the time of listing in 2014, its distribution has a greater capacity to moderate extinction risk.

4.4.3. Abundance

Relative Abundance: DeVantier and Turak (2017) characterized abundances of over 600 Indo-Pacific reef-building coral species in 31 Veron ecoregions from the Red Sea to Fiji, as further described in Section 4.1.3 above. *Acropora pharaonis* was recorded in 3 of the 31 ecoregions. Within those 3 ecoregions, it had a mean overall abundance of 64.52 (Very Common), ranging from 23.26

(Common) in the Red Sea South Ecoregion to 124.14 (Near Ubiquitous) in the Red Sea North-central Ecoregion. The mean overall abundance of *A. pharaonis* for all 31 ecoregions was 6.37 (Uncommon, DeVantier and Turak 2017, Table S2), however most of the 28 ecoregions where it was not recorded appear to be outside its range. The Coral Traits Database (https://coraltraits.org/, accessed August 2022) lists *A. pharaonis*'s global relative abundance as "uncommon," but does not cite DeVantier and Turak (2017). Within its range, the relative abundance of *A. pharaonis* may vary locally from very rare to near ubiquitous. However, based on the above information, the rangewide relative abundance of *A. pharaonis* is common. Thus, current information indicates that *A. pharaonis* has a higher relative abundance (common) than we were aware of at the time of listing in 2014 (uncommon).

Absolute Abundance. Based on *A. pharaonis'*s distribution and relative abundance, NMFS (2014) estimated the absolute abundance of *A. pharaonis* to be at least millions of colonies. However, since then we have learned that the species has a broader geographic distribution, a broader depth distribution, and a higher relative abundance. Based on the updated information, *A. pharaonis*'s absolute abundance is likely to be at least tens of millions of colonies. Thus, current information indicates that *A. pharaonis* has a higher absolute abundance (at least tens of millions) than we were aware of at the time of listing in 2014 (at least millions).

Abundance Trends. As described above in the general Threats Evaluation and below for threats to *A. pharaonis*, the most important threats (i.e., ocean warming, ocean acidification) have worsened since 2014, and substantial impacts to *Acropora* species have occurred, although no species-specific data are available for *A. pharaonis*. Based on the continued worsening of the most important threats, it is likely that *A. pharaonis* is decreasing in overall abundance (i.e., abundance across all the ecoregions that make up its range).

Relevance of Abundance to Status. Abundance is the key demographic factor considered in determining the status of coral species and in the listing of *A. pharaonis* in 2014. A low relative or absolute abundance, especially in combination with declining abundance, exacerbates a species' extinction risk because larger proportions of the population are likely to be exposed to any single disturbance. In contast, a higher relative or absolute abundance moderates a species' extinction risk because lower proportions of the population are likely to be exposed to any single disturbance (79 FR 53851). Since the relative and absolute abundances of *A. pharaonis* are both greater than we were aware of in at the time of listing in 2014, its abundance may have a greater capacity to moderate extinction risk.

4.4.4. Threats

This section provides an updated threats evaluation for *A. pharaonis*, focusing on the threats that contributed to its listing (79 FR 53851), including ocean warming, ocean acidification, disease, fishing, LBSP, predation, and inadequacy of existing regulatory mechanisms. In addition, current information indicates that collection and trade is also impacting the status of the species. A threats summary table is provided, including relative importance ratings for the threats, effects of threats since listing in 2014, and projected effects of threats in the foreseeable future.

Ocean Warming: As noted in Section 3.2.1 above, since listing in 2014, the effects of ocean warming on Indo-Pacific reef-building corals have substantially worsened. In response to the 2014–2017 series of warming-induced bleaching events, *Acropora* corals were generally the most impacted coral taxa in different locations around the Indo-Pacific (e.g., Hoogenboom et al. 2017, Frade et al 2018, Hughes et al. 2018a,b, Raymundo et al. 2019, Thinesh et al. 2019, Dietzel et al. 2020, Gilmour et al. 2022). Section 3.2.1 also describes how ocean warming is projected to greatly worsen in the foreseeable future (i.e., between now and 2100). In conclusion, the current information indicates that *A. pharaonis* continues to be highly susceptible to ocean warming, that this threat has substantially worsened since listing in 2014, and that it will greatly worsen in the foreseeable future (Table 7).

Ocean Acidification: As noted in Section 3.2.2 above, since listing in 2014, the effects of ocean acidification on Indo-Pacific reef-building corals have worsened. Generally, ocean acidification results in decreased growth and calcification rates in *Acropora* species, which are typically absent from coral communities existing in naturally low pH waters (Brainard et al. 2011, 79 FR 53851, Smith et al. 2020, Evenson et al. 2021, Hill and Hoogenboom 2022). Section 3.2.2 also describes how ocean acidification is projected to greatly worsen in the foreseeable future. In conclusion, the current information indicates that *A. pharaonis* continues to be susceptible to ocean acidification, that this threat has worsened since listing in 2014, and that it will greatly worsen in the foreseeable future (Table 7).

Disease: As noted in Section 3.2.3 above, since listing in 2014, the effects of disease on Indo-Pacific corals have increased, mainly in response to the 2014–2017 bleaching events. *Acropora* species are susceptible to most of the diseases that infect coral, and are more commonly affected by acute and lethal diseases ("white diseases" or tissue loss) than other corals. The reduction of coral populations by disease leads to negative synergisms, as it reduces *Acropora* reproductive output and can lead to recruitment failure, making population recovery very difficult (Brainard et al. 2011, 79 FR 53851, Hobbs et al. 2015, Aeby et al. 2020, Howells et al. 2020). Section 3.2.3 also describes how disease is projected to substantially worsen in the foreseeable future. In conclusion, the current information indicates that *A. pharaonis* continues to be susceptible to disease, that this threat has worsened since listing in 2014, and that it will substantially worsen in the foreseeable future (Table 7).

Fishing: As noted in Section 3.2.4 above, since listing in 2014, the direct and indirect effects of fishing on Indo-Pacific corals have continued, likely intensifying in some locations while lessening in others due to various factors. Branching, fast-growing corals such as most *Acropora* species may be more susceptible than other corals to damage by fishing gear because of their morphology, and to the trophic effects of fishing because of increased competition for space (Brainard et al. 2011, 79 FR 53851). Section 3.2.4 also describes how fishing is projected to substantially worsen in the foreseeable future. In conclusion, the current information indicates that *A. pharaonis* continues to be susceptible to fishing, that this threat has continued since listing in 2014, and that it will substantially worsen in the foreseeable future (Table 7).

LBSP: As noted in Section 3.2.5 above, since listing in 2014, the effects of LBSP on Indo-Pacific corals have continued, likely intensifying in some locations while lessening in others due to various factors. Generally, *Acropora* species are relatively susceptible to sediment and nutrients, compared to other reef-building coral taxa (Brainard et al. 2011, 79 FR 53851, Carlson et al. 2019, Tuttle and Donahue 2022). Section 3.2.5 also describes how LBSP is projected to substantially worsen in the foreseeable future. In conclusion, the current information indicates that *A. pharaonis* continues to be susceptible to LBSP, that this threat has continued since listing in 2014, and that it will substantially worsen in the foreseeable future (Table 7).

Predation: As noted in Section 3.2.6 above, since listing in 2014, the effects of predation on Indo-Pacific corals have increased, mainly because the 2014–2017 bleaching events resulted in more favorable conditions for predators such as COTS. *Acropora* species are highly susceptible to most predators that prey on coral, including COTS, a variety of snails including *Drupella*, butterflyfish, and fireworms. When *Acropora* populations are greatly reduced by other threats such as warming-induced bleaching or disease, predation can lead to collapse or lack of recovery (Brainard et al. 2011, 79 FR 53851, Keesing et al. 2019, Tkachenko and Huang 2022). Section 3.2.6 also describes how predation is projected to substantially worsen in the foreseeable future. In conclusion, the current information indicates that *A. pharaonis* continues to be susceptible to predation, that this threat has worsened since listing in 2014, and that it will substantially worsen in the foreseeable future (Table 7).

Collection and Trade: Although collection and trade did not contribute to the listing of *A. pharaonis* (79 FR 53851), the following information indicates that this threat is likely impacting the status of the species. As noted in Section 3.2.7 above, since listing in 2014, the effects of collection and trade on Indo-Pacific corals have continued. According to the CITES database, between 1985 and 2017, over 17 million *Acropora* units were globally imported and exported. These units were not identified to species, thus likely included an undeterminable number of unidentified *A. pharaonis*. In addition, the database also records that between 2009 and 2011, 50 to 500 *A. pharaonis* units were globally imported and exported annually (NMFS 2022a). Because of the growing popularity of "thick branching" *Acropora* species such as *A. pharaonis* in the marine aquarium trade as well as the ongoing and projected growth in the industry, collection and trade may increasingly impact the status of *A. pharaonis*. Section 3.2.7 also describes how collection and trade is projected to substantially worsen in the foreseeable future. In conclusion, the current information indicates that *A. pharaonis* is susceptible to collection and trade, that this threat has continued since listing in 2014, and that it will substantially worsen in the foreseeable future (Table 7).

Sea-level Rise: As noted in Section 3.2.8 above, since listing in 2014, sea-level rise has likely been too gradual to result in measurable effects on Indo-Pacific reef-building corals. In those cases where earthquakes have resulted in substrate uplift resembling sea-level rise, these substrates have been colonized by rapidly-growing corals like *Acropora* species. In conclusion, as in the final rule, the current information indicates that *A. pharaonis* is not susceptible to sea-level rise, that there have been no detectable trends in the effects of this threat since listing in 2014, but that it will worsen in the foreseeable future (Table 7).

Regulatory Mechanisms: As noted in Section 3.2.9 above, since listing in 2014, some progress has been made with GHG management as well as controlling local threats although existing regulatory mechanisms are still inadequate to control any of the threats. Section 3.2.9 also describes how it is unlikely that regulatory mechanisms will be improved to the point where they are adequate to control any of the threats in the foreseeable future. In conclusion, the current information indicates that existing regulatory mechanisms remain inadequate to control any threat to *A. pharaonis*, and that improvement is unlikely in the foreseeable future (Table 7).

Threats Conclusion for *A. pharaonis*: Since *A. pharaonis* was listed in 2014, many of the threats to the species have worsened. Especially concerning is that the most important threat to the species, ocean warming, has substantially worsened. In addition, all threats are projected to worsen in the foreseeable future, with the possible exception of regulatory mechanisms, which may continue to improve but also are likely to remain inadequate for controlling any of the threats (Table 7).

Although the final rule rated the relative importance of threats to the world's reef-building corals (Table 2), it did not apply those ratings to *A. pharaonis* (79 FR 53851). Instead, the final rule concluded that *A. pharaonis* is highly susceptible to ocean warming and susceptible to ocean acidification, disease, fishing, LBSP, and predation, while regulatory mechanisms were inadequate for controlling any threat (79 FR 53851). However, as summarized above, we now have more genus-specific and species-specific information available on the importance of each threat to *Acropora* species and *A. pharaonis*, respectively. Based on the general importance ratings of the threats to Indo-Pacific reef-building corals (Table 3) and the genus-specific and species-specific information above, we conclude that the relative importance ratings of each threat to Indo-Pacific corals apply to *A. pharaonis*. In addition, the observed threat trends since 2014 and projected threat trends in the foreseeable future are provided (Table 7).

Table 7. Summary of threats evaluation for *A. pharaonis*. For each threat, relative importance to the extinction risk of the species, observed trend since 2014, and projected trend in the foreseeable future are provided.

Threat (listing factor)	Importance	Observed Trend in Effects Since 2014	Projected Trend in Effects to 2100
Ocean Warming (Factor E)	Very High	Substantially worsened	Greatly worsen
Ocean Acidification (Factor E)	High	Worsened	Greatly worsen
Disease (Factor C)	High	Worsened	Substantially worsen
Fishing (Factor A)	Medium	Continued	Substantially worsen
LBSP (Factors A and E)	Low-Medium	Continued	Substantially worsen
Predation (Factor C)	Low-Medium	Worsened	Substantially worsen
Collection and Trade (Factor B)	Low-Medium	Continued	Substantially worsen
Sea-level Rise (Factor E)	Low	No detectable trends	Worsen
Inadequacy of Existing Regulatory Mechanisms (Factor D)	High	Some improvement but still inadequate	Improvement but likely still inadequate

4.4.5. Conclusion

As explained in the 2014 final listing rule (79 FR 53851), a species' vulnerability to extinction results from the combination of its spatial (i.e., distribution) and demographic (i.e., abundance) characteristics, threat susceptibilities, and consideration of the baseline environment and future projections of threats. *Acropora pharaonis* was listed as threatened in 2014 because of it limited geographic distribution restricted largely to the Red Sea and Arabian Gulf, high susceptibility to ocean warming, susceptibilities to ocean acidification, fishing, LBSP, disease, and predation, inadequate regulatory mechanisms, declining baseline conditions, and projected worsening of threats (79 FR 53851).

Since 2014, we have learned that *A. pharaonis* has: (1) a broader geographic distribution (20 instead of 19 Veron ecoregions); (2) a broader depth distribution (2–44 m instead of 5–25 m); (3) a higher relative abundance (common instead of uncommon); and (4) a higher absolute abundance (at least tens of millions of colonies instead of at least millions of colonies). That is, *A. pharaonis* is more broadly distributed and more abundant than we believed in 2014, and thus may have a higher capacity to moderate the effects of the threats, as explained in the Relevance of Distribution/Abundance to Status sections above.

Since 2014, the effects of ocean warming have substantially worsened, and the effects of most other threats have worsened as well. All threats are projected to substantially worsen under current global GHG regulatory mechanisms, which would result in global warming of 2.6–3.4°C above the pre-industrial baseline by 2100 (see Fig. 4 in Section 3.1 above). Even if the goal of the Paris Agreement is achieved (i.e., limiting global warming to 1.5°C above pre-industrial by 2100), the threats would become much worse than they are currently (Dixon et al. 2022), likely preventing the recovery of *A. pharaonis*. Current regulatory mechanisms are grossly inadequate, especially GHG management.

In conclusion, the above information shows that *A. pharaonis* is more broadly distributed and more abundant than we believed in 2014, but that the threats have worsened and that collection and trade is also an important threat to the species. Especially concerning is that the most important threat to the species, ocean warming, has substantially worsened since the species was listed in 2014. The other important threats to the species, including ocean acidification, disease, fishing, LBSP, predation, and collection and trade have also either worsened or continued since 2014. While there has been some progress with regulatory mechanisms, primarily because of the 2016 Paris Agreement, regulatory mechanisms for both global and local threats are still inadequate. However, the species' distribution is broader and its abundance is greater than we were aware of at the time of listing in 2014, both of which are key factors for moderating threats.

4.5. *Acropora retusa* (Dana 1846)

4.5.1. Biology

Taxonomy. This species was originally described as *Madrepora retusa* (Dana 1846), then assigned to the genus *Acropora* (Verrill 1902). The species name was little used since the original description until Wallace's (1999) *Acropora* revision, and subsequent inclusion in the Corals of the World books (Veron 2000) and website (http://www.coralsoftheworld.org/, accessed August 2022). Additional taxonomic details are provided in Wallace et al. (2012), and the species is accepted by WoRMS (Hoeksma and Cairns 2021).

Morphology. Colonies of *A. retusa* are flat plates with short, thick finger-like branches. Branches look spiky because radial corallites are variable in length, giving the species rougher-looking branches than other digitate *Acropora* species. Colonies are typically brown or green in color (Fig. 13). Corallites are tubular and thick walled. Similar *Acropora* species and key differences are described in Fenner and Burdick (2016) and Fenner (2020a).

Figure 13. *Acropora retusa*, showing colony and branch morphology. Photos from Tutuila, American Samoa (photos copyright, Doug Fenner).

Habitat. *Acropora retusa* occurs primarily on shallow forereefs and other shallow, high-energy environments (Veron et al. 2016). The Coral Traits Database (https://coraltraits.org/, accessed August 2022) lists *A. retusa*'s water clarity preference as "clear," and wave exposure preference as "exposed."

Life History. Little information is available on the life history of *A. retusa*. Generally, *Acropora* species have rapid skeletal growth and low tolerance to stress, and all are hermaphroditic broadcast spawners (Brainard et al. 2011). As noted in the *A. globiceps* life history section above, all 37 *Acropora* species (which did not include A. *retusa*) in Darling et al.'s (2012) global coral life history study were classified as "competitive species," based on broadcast spawning, rapid skeletal growth, and branching colony morphology. These life history characteristics allow *Acropora* species to recruit quickly to available substrate and successfully compete for space, but also make them susceptible to disturbance, thus they typically are only dominant in ideal conditions (Darling et al. 2012).

4.5.2. Distribution

Geographic Distribution. *Acropora retusa* has a relatively broad geographic distribution (the third-most broadly distributed of the 15 species reviewed in this document after *A. globiceps* and *M. australiensis*), occurring in 35 MEOWs (Fig. 14), based on information in NMFS (2022c). The current information indicates that *A. retusa* occurs in 35 MEOWs, the same number that we were aware of at the time of listing in 2014, but with two changes: We no longer consider *A. retusa* to occur in the Mariana Islands MEOW because the existing records appear to be of a different or undescribed species, and we now have records of *A. retusa* from the Chagos MEOW (NMFS 2022c). The distribution of the species within U.S. waters is described below.

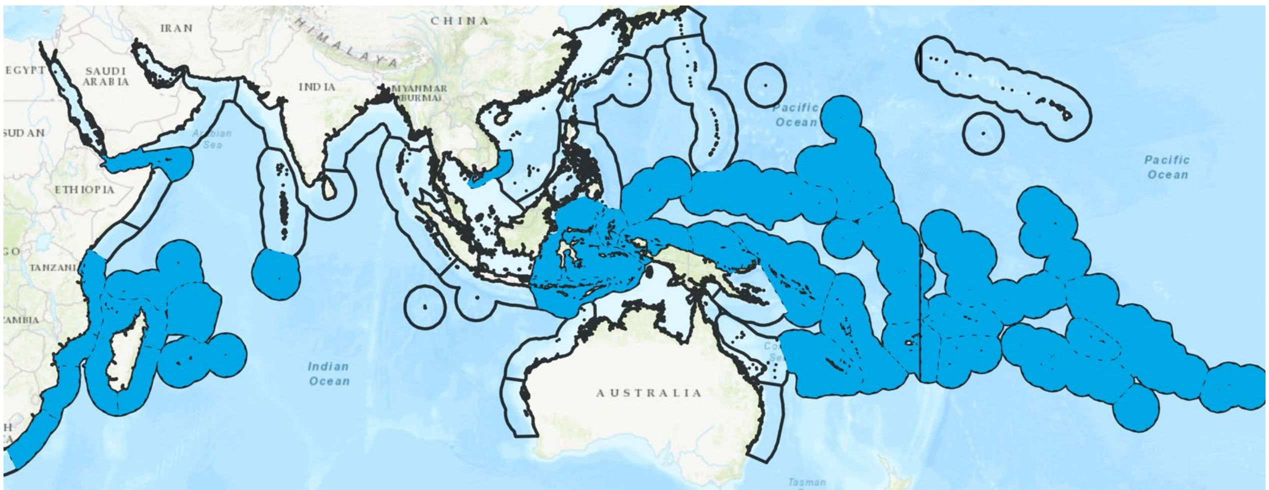


Figure 14. Geographic distribution of *A. retusa*.

Depth Distribution. *Acropora retusa* has a relatively broad depth range of 0–29 m. It has been recorded from 0 to 19.5 m of depth in American Samoa (NMFS 2022b), and at 29 m elsewhere in the Pacific (Coral Traits Database, https://coraltraits.org/, accessed August 2022). Thus, current information indicates that *A. retusa* has a much greater depth range (0–29 m) than we were aware of at the time of listing in 2014 (0-5 m).

U.S. Distribution. *Acropora retusa* occurs on Tutuila, Ofu, Olosega, and Rose Atoll in American Samoa, and on Wake Atoll in PRIA, as described in more detail in NMFS (2022b). American Samoa is within the Samoa MEOW, and Wake Atoll is within the Marshall Islands MEOW (Spalding et al. 2007).

Relevance of Distribution to Status. Geographic and depth distributions were the key spatial factors considered in determining the status of coral species and in the listing of *A. retusa* in 2014. A narrow geographic or depth distribution exacerbates a species' extinction risk because larger proportions of the population are likely to be exposed to any single disturbance. In contrast, a broad overall distribution moderates a species' extinction risk because the population is distributed across a range of geographic areas and depths, and thus lower proportions of the populations are likely to be exposed to any single disturbance. For example, one reason that *A. retusa* was listed was because the information available at that time indicated a narrow depth distribution of 0–5 m (79

FR 53851). Since the depth distribution of *A. retusa* is much greater (0–28.5 m) than we were aware of at the time of listing in 2014, its distribution has a greater capacity to moderate extinction risk.

4.5.3. Abundance

Relative Abundance: DeVantier and Turak (2017) characterized abundances of over 600 Indo-Pacific reef-building coral species in 31 Veron ecoregions from the Red Sea to Fiji, as further described in Section 4.1.3 above. *Acropora retusa* was recorded in 5 of the 31 ecoregions. Within those 5 ecoregions, it had a mean overall abundance of 3.86 (Uncommon), ranging from 1.03 (Uncommon) in the Vietnam South Ecoregion to 9.68 (Uncommon) in the Socotra Archipelago Ecoregion. The mean overall abundance of *A. retusa* for all 31 ecoregions was 0.55 (Rare, DeVantier and Turak 2017, Table S2), and most of the 26 ecoregions where it was not recorded appear to be within its range. In French Polynesia (outside the area surveyed by DeVantier and Turak 2017), *A. retusa* is one of the most common reef coral species (Lantz et al. 2017), making up one-third of all adult *Acropora* colonies in some locations (Lenihan et al. 2011). In addition, in South Africa (also outside the area surveyed by DeVantier and Turak 2017), *A. retusa* is common (Veron et al. 2016). The Coral Traits Database (https://coraltraits.org/, accessed August 2022) lists *A. retusa*'s global relative abundance as "uncommon," but does not cite DeVantier and Turak (2017), Lantz et al. (2017), or Veron et al. (2016). Within its range, the relative abundance of *A. retusa* may vary locally from very rare to at least common. However, based on the above information, the rangewide relative abundance of *A. retusa* is rare to uncommon.

Absolute Abundance. Based on *A. retusa's* distribution and relative abundance, NMFS (2014) estimated the absolute abundance of *A. retusa* to be at least millions of colonies. Dietzel et al. (2021) estimated its absolute abundance at 540 million colonies. Muir et al. (2022) argued that the data were unsuitable to provide such quantitative estimates, and Dietzel et al.'s (2022) reply agreed that better data are needed. Based on the updated information, *A. retusa*'s absolute abundance is likely to be at least hundreds of millions of colonies. Thus, current information indicates that *A. retusa* has a higher absolute abundance (at least hundreds of millions) than we were aware of at the time of listing in 2014 (at least millions).

Abundance Trends. When *A. retusa* was listed in 2014, it was thought to have a decreasing abundance trend across its range over at least the past several decades, based on overall declines in coral cover and the susceptibility of *A. retusa* to the worst threats. At that time, we were not aware of any time-series abundance trend data for this species (79 FR 53851). Since then, we learned of the National Park of American Samoa's (NPSA) coral species monitoring surveys conducted annually at 15 fixed and 15 temporary transects at 10–20 m depth from 2007 to 2019 on the north shore of Tutuila. On both the fixed and temporary transects, *A. retusa* cover ranged from zero to approximately 0.15% cover annually, with no apparent trend (NPSA 2020). The monitoring program is designed to monitor coral cover trends on the spatial scale of NPSA's Tutuila Unit (i.e., reef scale), and may or may not reflect abundance trends on larger spatial scales, such as island, archipelago or MEOW scales.

As described above in the general Threats Evaluation and below for threats to *A. retusa*, the most important threats (i.e., ocean warming, ocean acidification) have worsened since 2014, and substantial impacts to *Acropora* species including *A. retusa* have been documented. Based on the continued worsening in the most important threats, it is likely that *A. retusa* is decreasing in overall abundance (i.e., abundance across all the ecoregions that make up its range).

Relevance of Abundance to Status. Abundance is the key demographic factor considered in determining the status of coral species and in the listing of *A. retusa* in 2014. A low relative or absolute abundance, especially in combination with declining abundance, exacerbates a species' extinction risk because larger proportions of the population are likely to be exposed to any single disturbance. In contrast, a higher relative or absolute abundance moderates a species' extinction risk because lower proportions of the population are likely to be exposed to any single disturbance (79 FR 53851). Since the absolute abundance of *A. retusa* is greater than we were aware of in at the time of listing in 2014, its abundance may have a greater capacity to moderate extinction risk.

4.5.4. Threats

This section provides an updated threats evaluation for *A. retusa*, focusing on the threats that contributed to its listing (79 FR 53851), including ocean warming, ocean acidification, disease, fishing, LBSP, predation, and inadequacy of existing regulatory mechanisms. In addition, current information indicates that collection and trade is also impacting the status of the species. A threats summary table is provided, including relative importance ratings for the threats, effects of threats since listing in 2014, and projected effects of threats in the foreseeable future.

<u>Ocean Warming</u>: As noted in Section 3.2.1 above, since listing in 2014, the effects of ocean warming on Indo-Pacific reef-building corals in general have substantially worsened. In response to the 2014–2017 series of warming-induced bleaching events, *Acropora* corals were generally the most impacted coral taxa in different locations around the Indo-Pacific (e.g., Hoogenboom et al. 2017, Frade et al 2018, Hughes et al. 2018a,b, Raymundo et al. 2019, Thinesh et al. 2019, Dietzel et al. 2020, Gilmour et al. 2022). Section 3.2.1 also describes how ocean warming is projected to greatly worsen in the foreseeable future (i.e., between now and 2100).

With regard to impacts of this threat on *A. retusa*, on Kiritimati (Christmas) Atoll in the Line Islands of Kiribati, most *A. retusa* colonies in the lagoon were killed by the 2016 warming-induced bleaching event (Bowden-Kerby et al. 2021). On Moorea in French Polynesia, the largest, most fecund coral colonies of *Acropora* species including *A. retusa* had disproportionately high mortality in response to a warming event in 2019 (Speare et al. 2022). In conclusion, the current information indicates that *A. retusa* continues to be highly susceptible to ocean warming, that this threat has substantially worsened since listing in 2014, and that it will greatly worsen in the foreseeable future (Table 8).

<u>Ocean Acidification</u>: As noted in Section 3.2.2 above, since listing in 2014, the effects of ocean acidification on Indo-Pacific reef-building corals have worsened. Generally, *Acropora* species are susceptible to reduced calcification and skeletal growth from ocean acidification (Brainard et al. 2011, 79 FR 53851, Smith et al. 2020, Evenson et al. 2021, Hill and Hoogenboom 2022). Section 3.2.2 also describes how ocean acidification is projected to greatly worsen in the foreseeable future. In conclusion, the current information indicates that *A. retusa* continues to be susceptible to ocean acidification, that this threat has worsened since listing in 2014, and that it will greatly worsen in the foreseeable future (Table 8).

<u>Disease</u>: As noted in Section 3.2.3 above, since listing in 2014, the effects of disease on Indo-Pacific corals have increased, mainly in response to the 2014–2017 bleaching events. Generally, *Acropora* species are susceptible to most of the diseases that infect coral, and are more commonly affected by acute and lethal diseases than other corals (Brainard et al. 2011, 79 FR 53851, Hobbs et al. 2015, Aeby et al. 2020, Howells et al. 2020). Section 3.2.3 also describes how disease is projected to substantially worsen in the foreseeable future. In conclusion, the current information indicates that *A. retusa* continues to be susceptible to disease, that this threat has worsened since listing in 2014, and that it will substantially worsen in the foreseeable future (Table 8).

<u>Fishing</u>: As noted in Section 3.2.4 above, since listing in 2014, the direct and indirect effects of fishing on Indo-Pacific corals have continued, likely intensifying in some locations while lessening in others due to various factors. Generally, branching, fast-growing corals such as most *Acropora* species are susceptible to direct (i.e., damage by fishing gear because of their morphology) and

indirect (i.e., increased competition for space with algae) effects of fishing (Brainard et al. 2011, 79 FR 53851). Section 3.2.4 also describes how fishing is projected to substantially worsen in the foreseeable future. In conclusion, the current information indicates that *A. retusa* continues to be susceptible to fishing, that this threat has continued since listing in 2014, and that it will substantially worsen in the foreseeable future (Table 8).

LBSP: As noted in Section 3.2.5 above, since listing in 2014, the effects of LBSP on Indo-Pacific corals have continued, likely intensifying in some locations while lessening in others due to various factors. Generally, *Acropora* species are relatively susceptible to sediment and nutrients compared to other reef-building coral taxa (Brainard et al. 2011, 79 FR 53851, Carlson et al. 2019, Tuttle and Donahue 2022). Section 3.2.5 also describes how LBSP is projected to substantially worsen in the foreseeable future. In conclusion, the current information indicates that *A. retusa* continues to be susceptible to LBSP, that this threat has continued since listing in 2014, and that it will substantially worsen in the foreseeable future (Table 8).

Predation: As noted in Section 3.2.6 above, since listing in 2014, the effects of predation on Indo-Pacific corals have increased, mainly because the 2014–2017 bleaching events resulted in more favorable conditions for predators. Generally, *Acropora* species are relatively susceptible to predation compared to other reef-building coral taxa (Brainard et al. 2011, 79 FR 53851, Keesing et al. 2019, Tkachenko and Huang 2022). Section 3.2.6 also describes how predation is projected to substantially worsen in the foreseeable future. In conclusion, the current information indicates that *A. retusa* continues to be susceptible to predation, that this threat has worsened since listing in 2014, and that it will substantially worsen in the foreseeable future (Table 8).

Collection and Trade: Although collection and trade did not contribute to the listing of *A. retusa* (79 FR 53851), the following information indicates that this threat is likely impacting the status of the species. As noted in Section 3.2.7 above, since listing in 2014, the effects of collection and trade on Indo-Pacific corals have continued. According to the CITES database cited in Section 3.2.7, between 1985 and 2017, over 17 million *Acropora* units were globally imported and exported. These units were not identified to species, thus likely included an undeterminable number of unidentified *A. retusa*. In addition, the database also records that several thousand *A. retusa* units were globally imported and exported in 1992 (NMFS 2022a). Because of the ongoing and projected growth in the industry, collection and trade may increasingly impact the status of *A. retusa*. Section 3.2.7 also describes how collection and trade is projected to substantially worsen in the foreseeable future. In conclusion, the current information indicates that *A. retusa* is susceptible to collection and trade, that this threat has continued since listing in 2014, and that it will substantially worsen in the foreseeable future (Table 8).

Sea-level Rise: As noted in Section 3.2.8 above, since listing in 2014, sea-level rise has likely been too gradual to result in measurable effects on Indo-Pacific reef-building corals. In those cases where earthquakes have resulted in substrate uplift resembling sea-level rise, these substrates have been colonized by rapidly-growing corals like *Acropora* species. In conclusion, as in the final rule, the current information indicates that *A. retusa* is not susceptible to sea-level rise, that there have been no detectable trends in the effects of this threat since listing in 2014, but that it will worsen in the foreseeable future (Table 8).

Regulatory Mechanisms: As noted in Section 3.2.9 above, since listing in 2014, some progress has been made with GHG management as well as controlling local threats although existing regulatory mechanisms are still inadequate to control any of the threats. Section 3.2.9 also describes how it is unlikely that regulatory mechanisms will be improved to the point where they are adequate to control any of the threats in the foreseeable future. In conclusion, the current information indicates that existing regulatory mechanisms remain inadequate to control any threat to *A. retusa*, and that improvement is unlikely in the foreseeable future (Table 8).

Threats Conclusion for *A. retusa*: Since *A. retusa* was listed in 2014, many of the threats to the species have worsened. Especially concerning is that the most important threat to the species, ocean warming, has substantially worsened. In addition, all threats are projected to worsen in the foreseeable future, with the possible exception of regulatory mechanisms, which may continue to improve but also are likely to remain inadequate for controlling any of the threats (Table 8).

Although the final rule rated the relative importance of threats to the world's reef-building corals (Table 2), it did not apply those ratings to *A. retusa* (79 FR 53851). Instead, the final rule concluded that *A. retusa* is highly susceptible to ocean warming and susceptible to ocean acidification, disease, fishing, LBSP, and predation, while regulatory mechanisms were inadequate for controlling any threat (79 FR 53851). However, as summarized above, we now have more genus-specific and species-specific information available on the importance of each threat to *Acropora* species and *A. retusa*, respectively. Based on the general importance ratings of the threats to Indo-Pacific reef-building corals (Table 3) and the genus-specific and species-specific information above, we conclude that the relative importance ratings of each threat to Indo-Pacific corals apply to *A. retusa*. In addition, the observed threat trends since 2014 and projected threat trends in the foreseeable future are provided (Table 8).

Table 8. Summary of threats evaluation for *A. retusa*. For each threat, relative importance to the extinction risk of the species, observed trend since 2014, and projected trend in the foreseeable future are provided.

Threat (listing factor)	**Importance**	**Observed Trend in Effects Since 2014**	**Projected Trend in Effects to 2100**
Ocean Warming (Factor E)	Very High	Substantially worsened	Greatly worsen
Ocean Acidification (Factor E)	High	Worsened	Greatly worsen
Disease (Factor C)	High	Worsened	Substantially worsen
Fishing (Factor A)	Medium	Continued	Substantially worsen
LBSP (Factors A and E)	Low-Medium	Continued	Substantially worsen
Predation (Factor C)	Low-Medium	Worsened	Substantially worsen
Collection and Trade (Factor B)	Low-Medium	Continued	Substantially worsen
Sea-level Rise (Factor E)	Low	No detectable trends	Worsen
Inadequacy of Existing Regulatory Mechanisms (Factor D)	High	Some improvement but still inadequate	Improvement but likely still inadequate

4.5.5. Conclusion

As explained in the 2014 final listing rule (79 FR 53851), a species' vulnerability to extinction results from the combination of its spatial (i.e., distribution) and demographic (i.e., abundance) characteristics, threat susceptibilities, and consideration of the baseline environment and future projections of threats. *Acropora retusa* was listed as threatened in 2014 because of its limited depth distribution, low abundance, high susceptibility to ocean warming, susceptibilities to ocean acidification, fishing, LBSP, disease, and predation, inadequate regulatory mechanisms, declining baseline conditions, and projected worsening of threats (79 FR 53851).

Since 2014, we have learned that *A. retusa* has: (1) a much broader depth distribution (0–29 m instead of 0–5 m); and (2) higher absolute abundance (at least hundreds of millions of colonies instead of at least millions of colonies) than we believed in 2014. That is, *A. retusa* is more broadly distributed and more abundant than we believed in 2014, and thus may have a higher capacity to moderate the effects of the threats, as explained in the Relevance of Distribution/Abundance to Status sections above.

Since 2014, the effects of ocean warming have substantially worsened, and the effects of most other threats have worsened as well. All threats are projected to substantially worsen under current global GHG regulatory mechanisms, which would result in global warming of 2.6–3.4°C above the pre-industrial baseline by 2100 (see Fig. 4 in Section 3.1 above). Even if the goal of the Paris Agreement is achieved (i.e., limiting global warming to 1.5°C above pre-industrial by 2100), the threats would become much worse than they are currently (Dixon et al. 2022), likely preventing the recovery of *A. retusa*. Current regulatory mechanisms are grossly inadequate, especially GHG management.

In conclusion, the above information shows that *A. retusa* is more broadly distributed and more abundant than we believed in 2014, but that the threats have worsened and that collection and trade is also an important threat to the species. Especially concerning is that the most important threat to the species, ocean warming, has substantially worsened since the species was listed in 2014. The other important threats to the species, including ocean acidification, disease, fishing, LBSP, predation, and collection and trade have also either worsened or continued since 2014. While there has been some progress with regulatory mechanisms, primarily because of the 2016 Paris Agreement, regulatory mechanisms for both global and local threats are still inadequate. However, the species' depth distribution is broader and its abundance is greater than we were aware of at the time of listing in 2014, both of which are key factors for moderating threats.

4.6. *Acropora rudis* (Rehburg 1892)

4.6.1. Biology

Taxonomy. This species was originally described as *Madrepora rudis* (Rehberg 1892), then assigned to the genus *Acropora* (Verrill 1902). Additional taxonomic details are provided in Wallace (1999) and Wallace et al. (2012). It is included in the Corals of the World books (Veron 2000) and website (http://www.coralsoftheworld.org/, accessed August 2022), and is accepted by WoRMS (Hoeksma and Cairns 2021).

Morphology. *Acropora rudis* colonies are up to a meter in diameter and have thick, tapering, cylindrical branches that mostly radiate from a central attachment. Axial corallites are dome-shaped with small openings. Radial corallites occur only on the upper surfaces of branches, while lower surfaces are smooth (Fig. 15). All corallites are projecting and tubular, with very thick walls and small opening in the center (Wallace 1999, Veron et al. 2016).

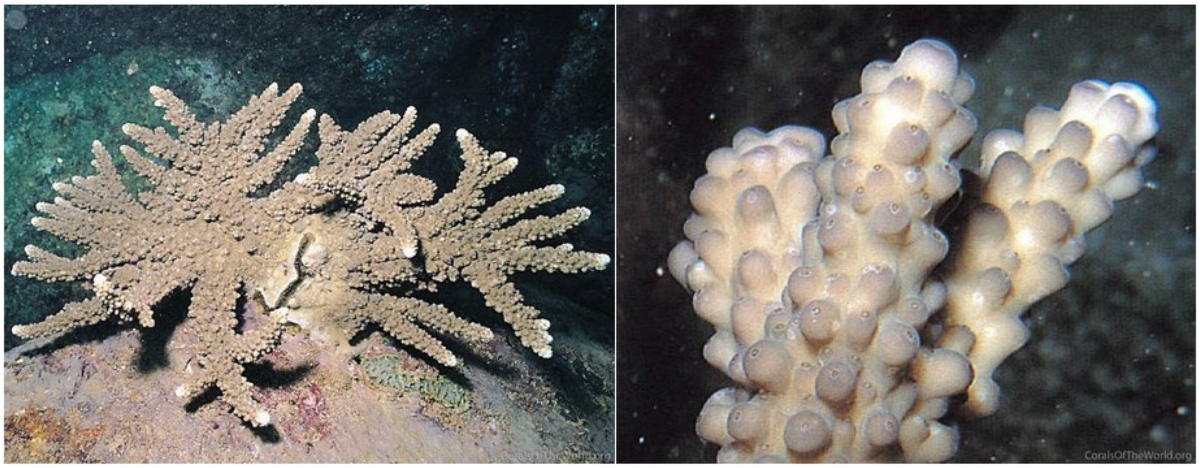


Figure 15. *Acropora rudis*, showing colony and branch morphology (Sri Lanka, Charlie Veron, Veron et al. 2016).

Habitat. *Acropora rudis* occurs on shallow to deep forereefs (Veron et al. 2016). The Coral Traits Database (https://coraltraits.org/, accessed August 2022) lists *A. rudis*'s water clarity preference as "clear", and wave exposure preference as "broad".

Life History. Little information is available on the life history of *A. rudis*. Generally, *Acropora* species have rapid skeletal growth and low tolerance to stress, and all are hermaphroditic broadcast spawners (Brainard et al. 2011). As noted in the *A. globiceps* life history section above, all 37 *Acropora* species (which did not include A. *rudis*) in Darling et al.'s (2012) global coral life history study were classified as "competitive species", based on broadcast spawning, rapid skeletal growth, and branching colony morphology. These life history characteristics allow *Acropora* species to recruit quickly to available substrate and successfully compete for space, but also make them susceptible to disturbance, thus they typically are only dominant in ideal conditions (Darling et al. 2012).

4.6.2. Distribution

Geographic Distribution. *Acropora rudis* has a relatively restricted geographic distribution, occurring in only nine MEOWs (Fig. 16) and does not occur in U.S. waters, based on information in NMFS (2022c). The current information indicates that *A. rudis* occurs in nine MEOWs, the same number that we were aware of at the time of listing in 2014 (NMFS 2022c). Its distribution includes the Maldives but is restricted largely to the northeastern Indian Ocean, which is an area projected to experience severe climate change and localized impacts within the foreseeable future.

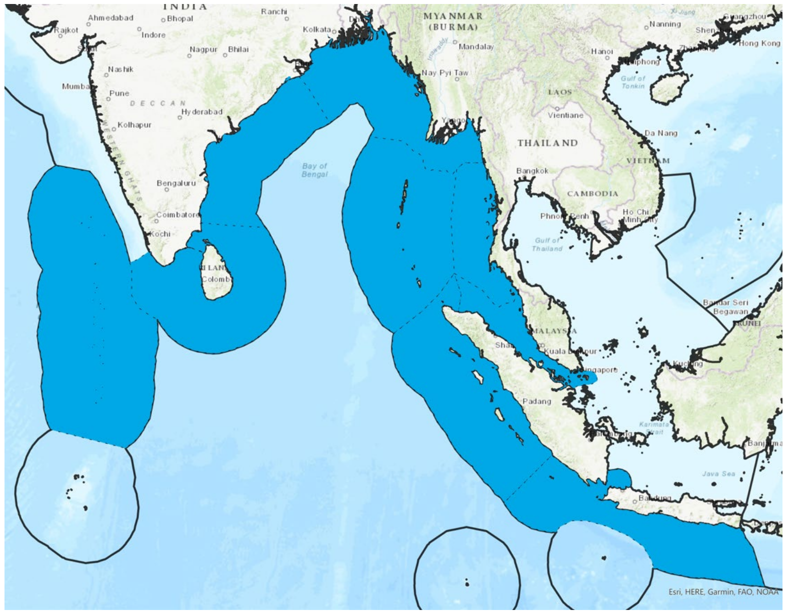


Figure 16. Geographic distribution of *A. rudis*.

Depth Distribution**.** *Acropora rudis* occurs on forereefs between 3 (Coral Traits Database https://coraltraits.org/, accessed August 2022) and 30 m (Turak and DeVantier 2019). Thus, current information indicates that *A. rudis* has a broader depth range (3–30 m) than we were aware of at the time of listing in 2014 (3–15 m).

Relevance of Distribution to Status. Geographic and depth distributions were the key spatial factors considered in determining the status of coral species and in the listing of *A. rudis* in 2014. A narrow geographic or depth distribution exacerbates a species' extinction risk because larger proportions of the population are likely to be exposed to any single disturbance. In contrast, a broad overall distribution moderates a species' extinction risk because the population is distributed across a range of geographic areas and depths, and thus lower proportions of the populations are likely to be exposed to any single disturbance. For example, one reason that *A. rudis* was listed was because the information available at that time indicated a narrow depth distribution of 3–15 m (79 FR 53851). Since the depth distribution of *A. rudis* is greater than we were aware of in at the time of listing in 2014, its distribution has a greater capacity to moderate extinction risk.

4.6.3. Abundance

Relative Abundance: DeVantier and Turak (2017) characterized abundances of over 600 Indo-Pacific reef-building coral species in 31 Veron ecoregions from the Red Sea to Fiji, as further described in Section 4.1.3 above. *Acropora rudis* was recorded in only the Andaman Sea Ecoregion, where it had an overall abundance of 9.26 (Uncommon). The mean overall abundance of *A. rudis* for all 31 ecoregions was 0.16 (Rare, DeVantier and Turak 2017, Table S2), however most of the 30 ecoregions where it was not recorded appear to be outside its range. The Coral Traits Database (https://coraltraits.org/, accessed August 2022) lists *A. rudis*'s global relative abundance as "uncommon", but does not cite DeVantier and Turak (2017). Based on the above information, the rangewide relative abundance of *A. rudis* is uncommon. Thus, current information indicates that *A. rudis* has a higher relative abundance (uncommon) than we were aware of at the time of listing in 2014 (rare).

Absolute Abundance. Based on *A. rudis*'s distribution and relative abundance, NMFS (2014) estimated the absolute abundance of *A. rudis* to be at least millions of colonies. The new information on its depth distribution and relative abundance are inadequate to revise the estimate of absolute abundance.

Abundance Trends. As described above in the general Threats Evaluation and below for threats to *A. rudis*, the most important threats (i.e., ocean warming, ocean acidification) have worsened since 2014, and substantial impacts to *Acropora* species have occurred, although no species-specific data are available for *A. rudis*. Based on the continued worsening in the most important threats, it is likely that *A. rudis* is decreasing in overall abundance (i.e., abundance across all the ecoregions that make up its range).

Relevance of Abundance to Status. Abundance is the key demographic factor considered in determining the status of coral species and in the listing of *A. rudis* in 2014. A low relative or absolute abundance, especially in combination with declining abundance, exacerbates a species' extinction risk because larger proportions of the population are likely to be exposed to any single disturbance. In contrast, a higher relative or absolute abundance moderates a species' extinction risk because lower proportions of the population are likely to be exposed to any single disturbance (79 FR 53851). Since the relative abundance of *A. rudis* is greater than we were aware of in at the time of listing in 2014, its abundance may have a greater capacity to moderate extinction risk.

4.6.4. Threats

This section provides an updated threats evaluation for *A. rudis*, focusing on the threats that contributed to its listing (79 FR 53851), including ocean warming, ocean acidification, disease, fishing, LBSP, predation, and inadequacy of existing regulatory mechanisms. In addition, current information indicates that collection and trade is also impacting the status of the species. A threats summary table is provided, including relative importance ratings for the threats, effects of threats since listing in 2014, and projected effects of threats in the foreseeable future.

Ocean Warming: As noted in Section 3.2.1 above, since listing in 2014, the effects of ocean warming on Indo-Pacific reef-building corals in general have substantially worsened. In response to the 2014–2017 series of warming-induced bleaching events, *Acropora* corals were generally the most impacted coral taxa in different locations around the Indo-Pacific (e.g., Hoogenboom et al. 2017, Frade et al 2018, Hughes et al. 2018a,b, Raymundo et al. 2019, Thinesh et al. 2019, Dietzel et al. 2020, Gilmour et al. 2022). Section 3.2.1 also describes how ocean warming is projected to greatly worsen in the foreseeable future (i.e., between now and 2100). In conclusion, the current information indicates that *A. rudis* continues to be highly susceptible to ocean warming, that this threat has substantially worsened since listing in 2014, and that it will greatly worsen in the foreseeable future (Table 9).

Ocean Acidification: As noted in Section 3.2.2 above, since listing in 2014, the effects of ocean acidification on Indo-Pacific reef-building corals have worsened. Generally, ocean acidification results in decreased growth and calcification rates in *Acropora* species, which are typically absent from coral communities existing in naturally low pH waters (Brainard et al. 2011, 79 FR 53851, Smith et al. 2020, Evenson et al. 2021, Hill and Hoogenboom 2022). Section 3.2.2 also describes how ocean acidification is projected to greatly worsen in the foreseeable future. In conclusion, the current information indicates that *A. rudis* continues to be susceptible to ocean acidification, that this threat has worsened since listing in 2014, and that it will greatly worsen in the foreseeable future (Table 9).

Disease: As noted in Section 3.2.3 above, since listing in 2014, the effects of disease on Indo-Pacific corals have increased, mainly in response to the 2014–2017 bleaching events. Generally, *Acropora* species are susceptible to most of the diseases that infect coral, and are more commonly affected by acute and lethal diseases than other corals (Brainard et al. 2011, 79 FR 53851, Hobbs et al. 2015, Aeby et al. 2020, Howells et al. 2020). Section 3.2.3 also describes how disease is projected to substantially worsen in the foreseeable future. In conclusion, the current information indicates that *A. rudis* continues to be susceptible to disease, that this threat has worsened since listing in 2014, and that it will substantially worsen in the foreseeable future (Table 9).

Fishing: As noted in Section 3.2.4 above, since listing in 2014, the direct and indirect effects of fishing on Indo-Pacific corals have continued, likely intensifying in some locations while lessening in others due to various factors. Generally, branching, fast-growing corals such as most *Acropora* species are susceptible to direct (i.e., damage by fishing gear because of their morphology) and indirect (i.e., increased competition for space with algae) effects of fishing (Brainard et al. 2011, 79 FR 53851). Section 3.2.4 also describes how fishing is projected to substantially worsen in the foreseeable future. In conclusion, the current information indicates that *A. rudis* continues to be susceptible to fishing, that this threat has continued since listing in 2014, and that it will substantially worsen in the foreseeable future (Table 9).

LBSP: As noted in Section 3.2.5 above, since listing in 2014, the effects of LBSP on Indo-Pacific corals have continued, likely intensifying in some locations while lessening in others due to various factors. Generally, *Acropora* species are relatively susceptible to sediment and nutrients compared to other reef-building coral taxa (Brainard et al. 2011, 79 FR 53851, Carlson et al. 2019, Tuttle and Donahue 2022). Section 3.2.5 also describes how LBSP is projected to substantially worsen in the foreseeable future. In conclusion, the current information indicates that *A. rudis* continues to be susceptible to LBSP, that this threat has continued since listing in 2014, and that it will substantially worsen in the foreseeable future (Table 9).

Predation: As noted in Section 3.2.6 above, since listing in 2014, the effects of predation on Indo-Pacific corals have increased, mainly because the 2014–2017 bleaching events resulted in more favorable conditions for predators such as COTS. Generally, *Acropora* species are relatively susceptible to predation compared to other reef-building coral taxa (Brainard et al. 2011, 79 FR 53851, Keesing et al. 2019, Tkachenko and Huang 2022). Section 3.2.6 also describes how predation is projected to substantially worsen in the foreseeable future. In conclusion, the current information indicates that *A. retusa* continues to be susceptible to predation, that this threat has worsened since listing in 2014, and that it will substantially worsen in the foreseeable future (Table 9).

Collection and Trade: Although collection and trade did not contribute to the listing of *A. retusa* (79 FR 53851), the following information indicates that this threat is likely impacting the status of the species. As noted in Section 3.2.7 above, since listing in 2014, the effects of collection and trade on Indo-Pacific corals have continued. According to the CITES database cited in Section 3.2.7, between 1985 and 2017, over 17 million *Acropora* units were globally imported and exported. These units were not identified to species, thus may have included an undeterminable number of unidentified *A. rudis*. In addition, the database also records that in 2014, 26 *A. rudis* units were globally imported and exported (NMFS 2022a). Because of the ongoing and projected growth in the industry, collection and trade may increasingly impact the status of *A. rudis*. Section 3.2.7 also describes how collection and trade is projected to substantially worsen in the foreseeable future. In conclusion, the current information indicates that *A. rudis* is susceptible to collection and trade, that this threat has continued since listing in 2014, and that it will substantially worsen in the foreseeable future (Table 9).

Sea-level Rise: As noted in Section 3.2.8 above, since listing in 2014, sea-level rise has likely been too gradual to result in measurable effects on Indo-Pacific reef-building corals. In those cases where earthquakes have resulted in substrate uplift resembling sea-level rise, these substrates have been colonized by rapidly-growing corals like *Acropora* species. In conclusion, as in the final rule, the current information indicates that *A. rudis* is not susceptible to sea-level rise, that there have been no detectable trends in the effects of this threat since listing in 2014, but that it will worsen in the foreseeable future (Table 9).

Regulatory Mechanisms: As noted in Section 3.2.9 above, since listing in 2014, some progress has been made with GHG management as well as controlling local threats although existing regulatory mechanisms are still inadequate to control any of the threats. Section 3.2.9 also describes how it is unlikely that regulatory mechanisms will be improved to the point where they are adequate to control any of the threats in the foreseeable future. In conclusion, the current information indicates that existing regulatory mechanisms remain inadequate to control any threat to *A. rudis*, and that improvement is unlikely in the foreseeable future (Table 9).

Threats Conclusion for *A. rudis*: Since *A. rudis* was listed in 2014, many of the threats to the species have worsened. Especially concerning is that the most important threat to the species, ocean warming, has substantially worsened. In addition, all threats are projected to worsen in the foreseeable future, with the possible exception of regulatory mechanisms, which may continue to improve but also are likely to remain inadequate for controlling any of the threats (Table 9).

Although the final rule rated the relative importance of threats to the world's reef-building corals (Table 2), it did not apply those ratings to *A. rudis* (79 FR 53851). Instead, the final rule concluded that *A. rudis* is highly susceptible to ocean warming and susceptible to ocean acidification, disease, fishing, LBSP, and predation, while regulatory mechanisms were inadequate for controlling any threat (79 FR 53851). However, as summarized above, we now have more genus-specific and species-specific information available on the importance of each threat to *Acropora* species and *A. rudis*, respectively. Based on the general importance ratings of the threats to Indo-Pacific reef-building corals (Table 3) and the genus-specific and species-specific information above, we conclude that the relative importance ratings of each threat to Indo-Pacific corals apply to *A. rudis*. In addition, the observed threat trends since 2014 and projected threat trends in the foreseeable future are provided (Table 9).

Table 9. Summary of threats evaluation for *A. rudis*. For each threat, relative importance to the extinction risk of the species, observed trend since 2014, and projected trend in the foreseeable future are provided.

Threat (listing factor)	**Importance**	**Observed Trend in Effects Since 2014**	**Projected Trend in Effects to 2100**
Ocean Warming (Factor E)	Very High	Substantially worsened	Greatly worsen
Ocean Acidification (Factor E)	High	Worsened	Greatly worsen
Disease (Factor C)	High	Worsened	Substantially worsen
Fishing (Factor A)	Medium	Continued	Substantially worsen
LBSP (Factors A and E)	Low-Medium	Continued	Substantially worsen
Predation (Factor C)	Low-Medium	Worsened	Substantially worsen
Collection and Trade (Factor B)	Low-Medium	Continued	Substantially worsen
Sea-level Rise (Factor E)	Low	No detectable trends	Worsen
Inadequacy of Existing Regulatory Mechanisms (Factor D)	High	Some improvement but still inadequate	Improvement but likely still inadequate

4.6.5. Conclusion

As explained in the 2014 final listing rule (79 FR 53851), a species' vulnerability to extinction results from the combination of its spatial (i.e., distribution) and demographic (i.e., abundance) characteristics, threat susceptibilities, and consideration of the baseline environment and future projections of threats. *Acropora rudis* was listed as threatened in 2014 because of its limited geographic distribution, low abundance, high susceptibility to ocean warming, susceptibilities to ocean acidification, fishing, LBSP, disease, and predation, inadequate regulatory mechanisms, declining baseline conditions, and projected worsening of threats (79 FR 53851).

Since 2014, we have learned that *A. rudis* has: (1) a broader depth distribution (3–30 m instead of 3–15 m); and (2) a higher relative abundance (uncommon instead of rare) than we believed in 2014. That is, *A. rudis* is more broadly distributed and more abundant than we believed in 2014, and thus may have a higher capacity to moderate the effects of the threats, as explained in the Relevance of Distribution/Abundance to Status sections above.

Since 2014, the effects of ocean warming have substantially worsened, and the effects of most other threats have worsened as well. All threats are projected to substantially worsen under current global GHG regulatory mechanisms, which would result in global warming of 2.6–3.4°C above the pre-industrial baseline by 2100 (see Fig. 4 in Section 3.1 above). Even if the goal of the Paris Agreement is achieved (i.e., limiting global warming to 1.5°C above pre-industrial by 2100), the threats would become much worse than they are currently (Dixon et al. 2022), likely preventing the recovery of *A. rudis*. Current regulatory mechanisms are grossly inadequate, especially GHG management.

In conclusion, the above information shows that *A. rudis* is more broadly distributed and more abundant than we believed in 2014, but that the threats have worsened and that collection and trade is also an important threat to the species. Especially concerning is that the most important threat to the species, ocean warming, has substantially worsened since the species was listed in 2014. The other important threats to the species, including ocean acidification,disease, fishing, LBSP, predation, and collection and trade have also either worsened or continued since 2014. While there has been some progress with regulatory mechanisms, primarily because of the 2016 Paris Agreement, regulatory mechanisms for both global and local threats are still inadequate. However, the species' distribution is broader and its abundance is greater than we were aware of at the time of listing in 2014, both of which are key factors for moderating threats.

4.7. *Acropora speciosa* (Quelch 1886)

4.7.1. Biology

Taxonomy. This species was originally described as *Madrepora speciosa* (Quelch 1886), then assigned to the genus *Acropora* (Verrill 1902). Similar to *A. globiceps* and *A. humilis* (see Section 3.1.1 above), *A. speciosa* was not distinguished from *A. granulosa* for many decades, which have similar appearances and habitats. The species were combined by Wallace (1978), but separated by Wallace and Wolstenholme (1998). Additional taxonomic details are provided in Wallace (1999) and Wallace et al. (2012). It is included in the Corals of the World books (Veron 2000) and website (http://www.coralsoftheworld.org/, accessed August 2022), and is accepted by WoRMS (Hoeksma and Cairns 2021).

Morphology. *Acropora speciosa* forms flat-topped colonies with small branches that have long smooth tips. Colonies are usually uniform grey-brown or pinkish in color (Fig. 17), up to 50 cm in diameter (Wallace 1999). As noted in Section 3.2.1. above, *A. speciosa* is very difficult to distinguish from *A. jacquelineae* in the water, but can be distinguished under the microscope based on skeletal characteristics (Fenner and Burdick 2016, Fenner 2020a).

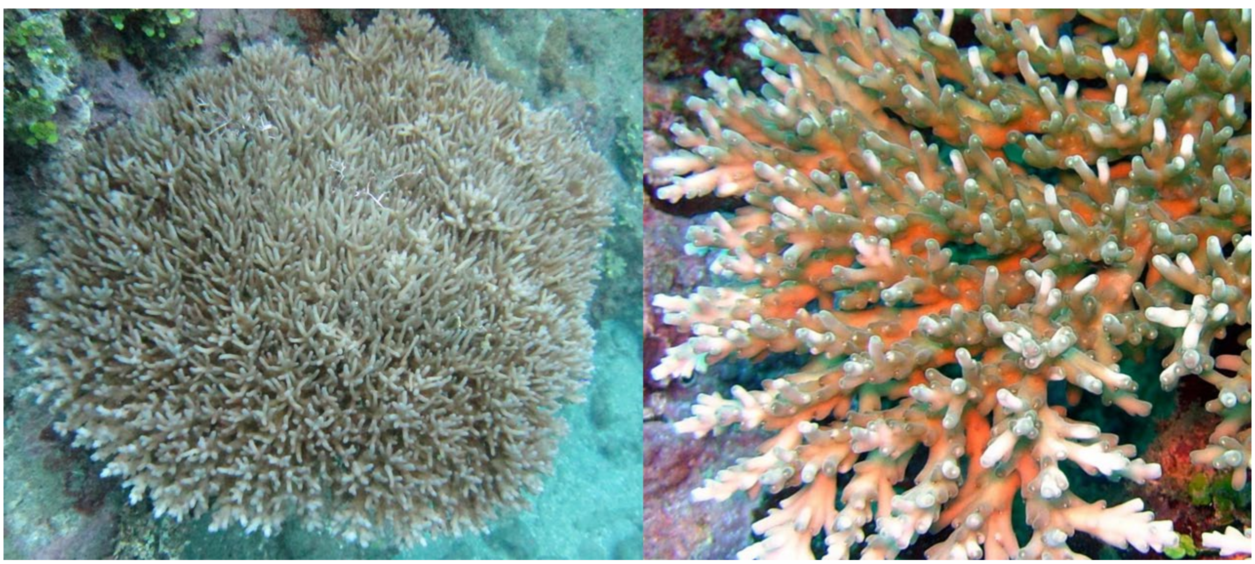


Figure 17. *Acropora speciosa*, showing colony and branch morphology. Photos from Tutuila, American Samoa (photos copyright, Doug Fenner).

Habitat. *Acropora speciosa* occurs on walls and steep slopes, usually deeper than 15 m but occasionally shallower where shaded conditions exist (Wallace and Wolstenholme 1998). The species is most often found at 30–60 m depth, and is rare at <30 m (Turak and DeVantier 2019), prompting Montgomery et al. (2021) to classify it as an "occasional deep specialist". The Coral Traits Database (https://coraltraits.org/, accessed August 2022) lists *A. speciosa*'s water clarity preference as "clear," and wave exposure preference as "protected."

In the final rule, the available information at that time indicated that *A. speciosa* was mainly limited to specialized habitat described as "lower reef slopes and walls, especially those characterized by clear water and high *Acropora* diversity on steep slopes." 79 FR 53851. However, mesophotic surveys conducted since then in American Samoa found colonies of the species on various types of rocky substrates, mostly isolated limestone mounds (Montgomery et al. 2019).

Life History. Little information is available on the life history of *A. speciosa*. Generally, *Acropora* species have rapid skeletal growth and low tolerance to stress, and all are hermaphroditic broadcast spawners (Brainard et al. 2011). As noted in the *A. globiceps* life history section above, all 37 *Acropora* species (which did not include A. *speciosa*) in Darling et al.'s (2012) global coral life history study were classified as "competitive species," based on broadcast spawning, rapid skeletal growth, and branching colony morphology. These life history characteristics allow *Acropora* species to recruit quickly to available substrate and successfully compete for space, but also make them susceptible to disturbance, thus they typically are only dominant in ideal conditions (Darling et al. 2012).

4.7.2. Distribution

Geographic Distribution. *Acropora speciosa* has a relatively broad distribution, occurring in 33 MEOWs (Fig. 18), based on information in NMFS (2022c). The current information indicates that *A. speciosa* occurs in three more MEOWs (Chagos, Phoenix/Tokelau/Northern Cook Islands, and Southern Cook/Austral Islands) than we were aware of at the time of listing in 2014 (NMFS 2022c). The distribution of the species within U.S. waters is summarized below.

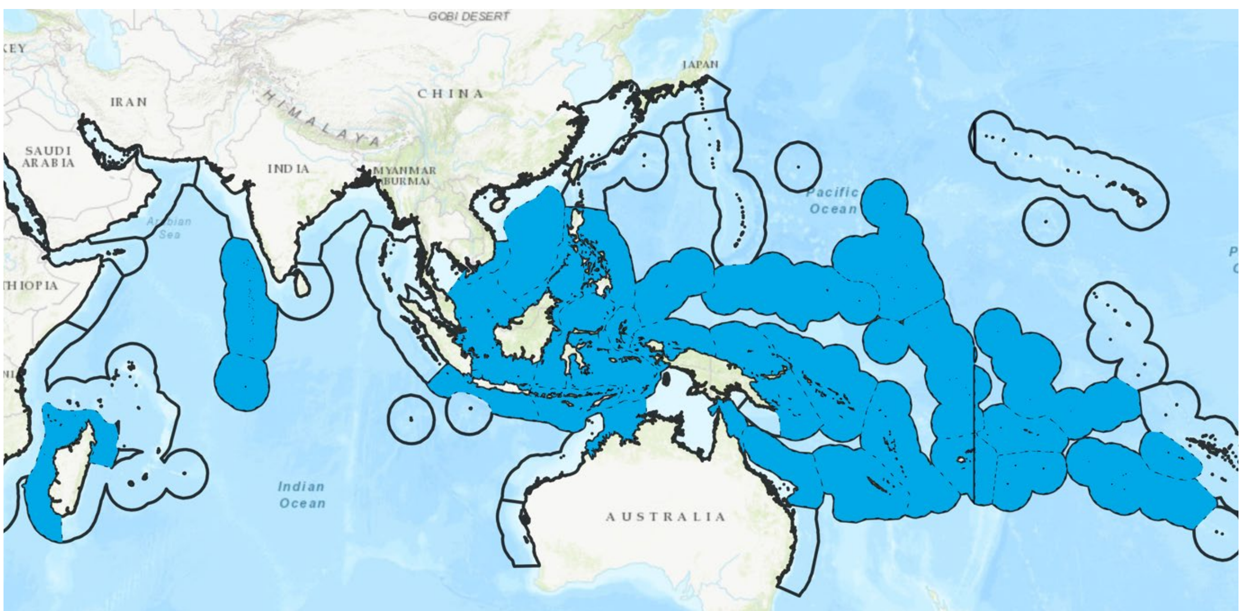


Figure 18. Geographic distribution of *A. speciosa*.

Depth Distribution. *Acropora speciosa* occurs from 12 m of depth (Coral Traits Database, https://coraltraits.org/, accessed August 2022) to 65 m of depth (Muir and Pichon 2019). Thus, current information indicates that *A. speciosa* has a broader depth range (12–65 m) than we were aware of at the time of listing in 2014 (12-40 m).

U.S. Distribution. *Acropora speciosa* occurs on Tutuila in American Samoa but has not been recorded elsewhere within U.S. waters (2022b). American Samoa is within the Samoa MEOW (Spalding et al. 2007).

Relevance of Distribution to Status. Geographic and depth distributions were the key spatial factors considered in determining the status of coral species and in the listing of *A. speciosa* in 2014. A narrow geographic or depth distribution exacerbates a species' extinction risk because larger proportions of the population are likely to be exposed to any single disturbance. In contrast, a broad overall distribution moderates a species' extinction risk because the population is distributed across a range of geographic areas and depths, and thus lower proportions of the populations are likely to be exposed to any single disturbance. In addition, distribution at mesophotic depths (>30 m) may moderate the impacts of threats against threats that are more severe in shallower reef environments such as warming (79 FR 53851). Since the depth distributions of *A. speciosa* is greater than we were aware of at the time of listing in 2014, its distribution has a greater capacity to moderate extinction risk.

4.7.3. Abundance

Relative Abundance: DeVantier and Turak (2017) characterized abundances of over 600 Indo-Pacific reef-building coral species in 31 Veron ecoregions from the Red Sea to Fiji, as further described in Section 4.1.3 above. *Acropora speciosa* was recorded in 17 of the 31 ecoregions. Within those 17 ecoregions, it had a mean overall abundance of 24.46 (Common), ranging from 0.34 (Rare) in the GBR North-central Ecoregion to 97.09 (Very Common) in the Sunda Shelf Ecoregion. The mean overall abundance of *A. speciosa* for all 31 ecoregions was 13.66 (Common, DeVantier and Turak 2017, Table S2), however some of the 14 ecoregions where it was not recorded may be outside its range. Another consideration is that *A. speciosa* may be relatively abundant at mesophotic depths. For example, mesophotic surveys in the Coral Triangle found that *A. speciosa* was one of the five most common *Acropora* species at 30–50 m (Turak and DeVantier 2019). The Coral Traits Database (https://coraltraits.org/, accessed August 2022) lists *A. speciosa*'s global relative abundance as "uncommon", but does not cite DeVantier and Turak (2017) or Turak and DeVantier (2019). Within its range, the relative abundance of *A. speciosa* may vary locally from very rare to at least very common. However, based on the above information, the rangewide relative abundance of *A. speciosa* is common. Thus, current information indicates that *A. speciosa* has a higher relative abundance (common) than we were aware of at the time of listing in 2014 (rare to uncommon).

Absolute Abundance. Absolute abundance is an estimate of the total number of colonies of a species that currently exist throughout its range. Based on information from Richards et al. (2008, 2019), *A. speciosa* had a population estimate of 10,942,000 colonies, and an effective population size of 1,204,000 colonies (79 FR 53851). However, *A. speciosa*'s distribution is larger than assumed by Richards et al. (2008, 2019). Dietzel et al. (2021) estimated its absolute abundance at 19.2 million colonies. Muir et al. (2022) argued that the data were unsuitable to provide such quantitative estimates, and Dietzel et al.'s (2022) reply agreed that better data are needed. Based on the updated information, *A. speciosa*'s absolute abundance is likely to be at least tens of millions of colonies.

Abundance Trends. As described above in the general Threats Evaluation and below for threats to *A. speciosa*, the most important threats (i.e., ocean warming, ocean acidification) have worsened since 2014, and substantial impacts to *Acropora* species have occurred, although no species-specific data are available for *A. speciosa*. Based on the continued worsening in the most important threats, it is likely that *A. speciosa* is decreasing in overall abundance (i.e., abundance across all the ecoregions that make up its range).

Relevance of Abundance to Status. Abundance is the key demographic factor considered in determining the status of coral species and in the listing of *A. speciosa* in 2014. A low relative or absolute abundance, especially in combination with declining abundance, exacerbates a species' extinction risk because larger proportions of the population are likely to be exposed to any single disturbance. In contrast, a higher relative or absolute abundance moderates a species' extinction risk because lower proportions of the population are likely to be exposed to any single disturbance (79 FR 53851). Since the relative abundance of *A. speciosa* is greater than we were aware of in at the time of listing in 2014, its abundance may have a greater capacity to moderate extinction risk.

4.7.4. Threats

This section provides an updated threats evaluation for *A. speciosa*, focusing on the threats that contributed to its listing (79 FR 53851), including ocean warming, ocean acidification, disease, fishing, LBSP, predation, and inadequacy of existing regulatory mechanisms. In addition, current information indicates that collection and trade is also impacting the status of the species. A threats summary table is provided, including relative importance ratings for the threats, effects of threats since listing in 2014, and projected effects of threats in the foreseeable future.

Ocean Warming: As noted in Section 3.2.1 above, since listing in 2014, the effects of ocean warming on Indo-Pacific reef-building corals in general have substantially worsened. In response to the 2014–2017 series of warming-induced bleaching events, *Acropora* corals were generally the most impacted coral taxa in different locations around the Indo-Pacific (e.g., Hoogenboom et al. 2017, Frade et al 2018, Hughes et al. 2018a,b, Raymundo et al. 2019, Thinesh et al. 2019, Dietzel et al. 2020, Gilmour et al. 2022). Section 3.2.1 also describes how ocean warming is projected to greatly worsen in the foreseeable future (i.e., between now and 2100).

A model based on species' responses to the 2016 bleaching event found that *A. speciosa* is at relatively low extinction risk from warming-induced bleaching because of its broad and deep depth distribution. Although *Acropora* species with more limited distributions are at greater extinction risk, the continued worsening of ocean warming also represents the key threat to the continued existence of *A. speciosa*. However, its distribution may provide a network of refuges in the future that will allow it to persist longer than species with more restricted distributions (Muir et al. 2017). In conclusion, the current information indicates that *A. speciosa* continues to be highly susceptible to ocean warming, that this threat has substantially worsened since listing in 2014, that it will greatly worsen in the foreseeable future (Table 10).

Ocean Acidification: As noted in Section 3.2.2 above, since listing in 2014, the effects of ocean acidification on Indo-Pacific reef-building corals have worsened. Generally, *Acropora* species are susceptible to reduced calcification and skeletal growth from ocean acidification (Brainard et al. 2011, 79 FR 53851, Smith et al. 2020, Evenson et al. 2021, Hill and Hoogenboom 2022). Section 3.2.2 also describes how ocean acidification is projected to greatly worsen in the foreseeable future. In conclusion, the current information indicates that *A. speciosa* continues to be susceptible to ocean acidification, that this threat has worsened since listing in 2014, and that it will greatly worsen in the foreseeable future (Table 10).

Disease: As noted in Section 3.2.3 above, since listing in 2014, the effects of disease on Indo-Pacific corals have increased, mainly in response to the 2014–2017 bleaching events. Generally, *Acropora* species are susceptible to most of the diseases that infect coral, and are more commonly affected by acute and lethal diseases than other corals (Brainard et al. 2011, 79 FR 53851, Hobbs et al. 2015, Aeby et al. 2020, Howells et al. 2020). Section 3.2.3 also describes how disease is projected to substantially worsen in the foreseeable future. In conclusion, the current information indicates that *A. speciosa* continues to be susceptible to disease, that this threat has worsened since listing in 2014, and that it will substantially worsen in the foreseeable future (Table 10).

Fishing: As noted in Section 3.2.4 above, since listing in 2014, the direct and indirect effects of fishing on Indo-Pacific corals have continued, likely intensifying in some locations while lessening in others due to various factors. Generally, branching, fast-growing corals such as most *Acropora* species are susceptible to direct (i.e., damage by fishing gear because of their morphology) and indirect (i.e., increased competition for space with algae) effects of fishing (Brainard et al. 2011, 79 FR 53851). Section 3.2.4 also describes how fishing is projected to substantially worsen in the foreseeable future. In conclusion, the current information indicates that *A. speciosa* continues to be susceptible to fishing, that this threat has continued since listing in 2014, and that it will substantially worsen in the foreseeable future (Table 10).

LBSP: As noted in Section 3.2.5 above, since listing in 2014, the effects of LBSP on Indo-Pacific corals have continued, likely intensifying in some locations while lessening in others due to various factors. Generally, *Acropora* species are relatively susceptible to sediment and nutrients, compared to other reef-building coral taxa (Brainard et al. 2011, 79 FR 53851). Section 3.2.5 also describes how LBSP is projected to substantially worsen in the foreseeable future. In conclusion, the current information indicates that *A. speciosa* continues to be susceptible to LBSP, that this threat has continued since listing in 2014, and that it will substantially worsen in the foreseeable future (Table 10).

Predation: As noted in Section 3.2.6 above, since listing in 2014, the effects of predation on Indo-Pacific corals have increased, mainly because the 2014–2017 bleaching events resulted in more favorable conditions for predators such as COTS. Generally, *Acropora* species are relatively susceptible to predation compared to other reef-building coral taxa (Brainard et al. 2011, 79 FR 53851, Keesing et al. 2019, Tkachenko and Huang 2022). Section 3.2.6 also describes how predation is projected to substantially worsen in the foreseeable future. In conclusion, the current information indicates that *A. speciosa* continues to be susceptible to predation, that this threat has worsened since listing in 2014, and that it will substantially worsen in the foreseeable future (Table 10).

Collection and Trade: Although collection and trade did not contribute to the listing of *A. speciosa* (79 FR 53851), the following information indicates that this threat is likely impacting the status of the species. As noted in Section 3.2.7 above, since listing in 2014, the effects of collection and trade on Indo-Pacific corals have continued. According to the CITES database cited in Section 3.2.7, between 1985 and 2017, over 17 million *Acropora* units were globally imported and exported. These units were not identified to species, thus likely included an undeterminable number of unidentified *A. speciosa*. In addition, the database also records that between 2003 and 2017, dozens to hundreds of *A. speciosa* units were globally imported and exported annually (NMFS 2022a). Because of the popularity of *A. speciosa* in the marine aquarium trade (Adams 2018, Chalias 2019c), as well as the ongoing and projected growth in the industry, collection and trade may increasingly impact the status of *A. speciosa*. Section 3.2.7 also describes how collection and trade is projected to substantially worsen in the foreseeable future. In conclusion, the current information indicates that *A. speciosa* is susceptible to collection and trade, that this threat has continued since listing in 2014, and that it will substantially worsen in the foreseeable future (Table 10).

Sea-level Rise: As noted in Section 3.2.8 above, since listing in 2014, sea-level rise has likely been too gradual to result in measurable effects on Indo-Pacific reef-building corals. In those cases where earthquakes have resulted in substrate uplift resembling sea-level rise, these substrates have been colonized by rapidly-growing corals like *Acropora* species. In conclusion, as in the final rule, the current information indicates that *A. speciosa* is not susceptible to sea-level rise, that there have been no detectable trends in the effects of this threat since listing in 2014, but that it will worsen in the foreseeable future (Table 10).

Regulatory Mechanisms: As noted in Section 3.2.9 above, since listing in 2014, some progress has been made with GHG management as well as controlling local threats although existing regulatory mechanisms are still inadequate to control any of the threats. Section 3.2.9 also describes how it is unlikely that regulatory mechanisms will be improved to the point where they are adequate to control any of the threats in the foreseeable future. In conclusion, the current information indicates that existing regulatory mechanisms remain inadequate to control any threat to *A. speciosa*, and that improvement is unlikely in the foreseeable future (Table 10).

Threats Conclusion for *A. speciosa*: Since *A. speciosa* was listed in 2014, many of the threats to the species have worsened. Especially concerning is that the most important threat to the species, ocean warming, has substantially worsened. In addition, all threats are projected to worsen in the foreseeable future, with the possible exception of regulatory mechanisms, which may continue to improve but also are likely to remain inadequate for controlling any of the threats (Table 10).

Although the final rule rated the relative importance of threats to the world's reef-building corals (Table 2), it did not apply those ratings to *A. speciosa* (79 FR 53851). Instead, the final rule concluded that *A. speciosa* is highly susceptible to ocean warming and susceptible to ocean acidification, disease, fishing, LBSP, and predation, while regulatory mechanisms were inadequate for controlling any threat (79 FR 53851). However, as summarized above, we now have more genus-specific and species-specific information available on the importance of each threat to *Acropora* species and *A. speciosa*, respectively. Based on the general importance ratings of the threats to Indo-Pacific reef-building corals (Table 3) and the genus-specific and species-specific information above, we conclude that the relative importance ratings of each threat to Indo-Pacific corals apply to *A. speciosa*. In addition, the observed threat trends since 2014 and projected threat trends in the foreseeable future are provided (Table 10).

Table 10. Summary of threats evaluation for *A. speciosa*. For each threat, relative importance to the extinction risk of the species, observed trend since 2014, and projected trend in the foreseeable future are provided.

Threat (listing factor)	**Importance**	**Observed Trend in Effects Since 2014**	**Projected Trend in Effects to 2100**
Ocean Warming (Factor E)	Very High	Substantially worsened	Greatly worsen
Ocean Acidification (Factor E)	High	Worsened	Greatly worsen
Disease (Factor C)	High	Worsened	Substantially worsen
Fishing (Factor A)	Medium	Continued	Substantially worsen
LBSP (Factors A and E)	Low-Medium	Continued	Substantially worsen
Predation (Factor C)	Low-Medium	Worsened	Substantially worsen
Collection and Trade (Factor B)	Low-Medium	Continued	Substantially worsen
Sea-level Rise (Factor E)	Low	No detectable trends	Worsen
Inadequacy of Existing Regulatory Mechanisms (Factor D)	High	Some improvement but still inadequate	Improvement but likely still inadequate

4.7.5. Conclusion

As explained in the 2014 final listing rule (79 FR 53851), a species' vulnerability to extinction results from the combination of its spatial (i.e., distribution) and demographic (i.e., abundance) characteristics, threat susceptibilities, and consideration of the baseline environment and future projections of threats. *Acropora speciosa* was listed as threatened in 2014 because of its specialized habitat, low abundance, high susceptibility to ocean warming, susceptibilities to ocean acidification, fishing, LBSP, disease, and predation, inadequate regulatory mechanisms, declining baseline conditions, and projected worsening of threats (79 FR 53851).

Since 2014, we have learned that *A. speciosa* has: (1) less specialized habitat (occurs on a variety of hard substrates not just walls and steeps slopes with certain characteristics); (2) a broader depth distribution (12–65 m instead of 12–40 m); and (3) a higher relative abundance (common instead of rare to uncommon) than we believed in 2014. That is, *A. speciosa* has less specialized habitat and is more broadly distributed and more abundant than we believed in 2014, and thus may have a higher capacity to moderate the effects of the threats, as explained in the Relevance of Distribution/Abundance to Status sections above.

Since 2014, the effects of ocean warming have substantially worsened, and the effects most other threats have worsened as well. All threats are projected to substantially worsen under current global GHG regulatory mechanisms, which would result in global warming of 2.6–3.4°C above the pre-industrial baseline by 2100 (see Fig. 4 in Section 3.1 above). Even if the goal of the Paris Agreement is achieved (i.e., limiting global warming to 1.5°C above pre-industrial by 2100), the threats would become much worse than they are currently (Dixon et al. 2022), likely preventing the recovery of *A. speciosa*. Current regulatory mechanisms are grossly inadequate, especially GHG management.

In conclusion, the above information shows that *A. speciosa* is more broadly distributed and more abundant than we believed in 2014, but that the threats have worsened and that collection and trade is also an important threat to the species. Especially concerning is that the most important threat to the species, ocean warming, has substantially worsened since the species was listed in 2014. The other important threats to the species, including ocean acidification,disease, fishing, LBSP, predation, and collection and trade have also either worsened or continued since 2014. While there has been some progress with regulatory mechanisms, primarily because of the 2016 Paris Agreement, regulatory mechanisms for both global and local threats are still inadequate. However, the species' distribution is broader and its abundance is greater than we were aware of at the time of listing in 2014, both of which are key factors for moderating threats.

4.8. *Acropora tenella* (Brook 1892)

4.8.1. Biology

Taxonomy. This species was originally described as *Madrepora tenella* (Brook 1892), then assigned to the genus *Acropora* (Verrill 1902). Additional taxonomic details are provided in Wallace (1999) and Wallace et al. (2012). It is included in the Corals of the World books (Veron 2000) and website (http://www.coralsoftheworld.org/, accessed August 2022), and is accepted by WoRMS (Hoeksma and Cairns 2021).

Morphology. *Acropora tenella* colonies are horizontal plates consisting of flattened branches. The branches usually diverge fan-wise in a regular pattern, but may form irregular tangles. Colonies are cream with white or blue branch ends (Fig. 19, Veron et al. 2016).

Figure 19. *Acropora tenella*, showing colony and branch morphology. Both photos taken on the GBR (Emre Turak; Veron et al. 2016).

Habitat. *Acropora tenella* is a mesophotic species and is most common at >40 m of depth (Turak and DeVantier 2019). In a detailed study of *A. tenella*, Muir et al. (2019) found that the species inhabits an extraordinary range of depths and habitats (e.g., exposed lower reef slopes, sheltered bays, and lagoons), including a reported depth of 110 m on an atoll lower reef slope in the Coral Sea, deeper than any other *Acropora* species. Elsewhere in the Pacific, other studies have found that *A. tenella* is common over rubble and sand in the upper mesophotic (Denis et al. 2019, Sinniger et al. 2019). The Coral Traits Database (https://coraltraits.org/, accessed August 2022) lists *A. tenella*'s water clarity preference as "clear", and wave exposure preference as "protected".

Life History. Some information is available on the life history of *A. tenella*. Reproductive studies of *A. tenella* show that broadcast spawning occurs seasonally similar to shallow *Acropora* species, but that *A. tenella* has longer gametogenic cycles (i.e., the formation and maturation of gametes) and lower fecundity than shallow *Acropora* species (Prasetia et al. 2016, 2017). Asexual reproduction via branch fragmentation is common in this species, as shown by extensive patches of unattached branches (Sinniger et al. 2019). Skeletal growth rate is estimated at 5–10 mm annually (Turak and DeVantier 2019). Generally, *Acropora* species have rapid skeletal growth and low tolerance to stress, and all are hermaphroditic broadcast spawners (Brainard et al. 2011). As noted in the *A. globiceps* life history section above, all 37 *Acropora* species (which did not include *A. tenella*) in Darling et al.'s (2012) global coral life history study were classified as "competitive species," based on broadcast spawning, rapid skeletal growth, and branching colony morphology. These life history characteristics allow *Acropora* species to recruit quickly to available substrate and successfully compete for space, but also make them susceptible to disturbance, thus they typically are only dominant in ideal conditions (Darling et al. 2012).

4.8.2. Distribution

Geographic Distribution. *Acropora tenella* has a relatively limited geographic distribution, occurring in 23 MEOWs (Fig. 20) and does not occur in U.S. waters, based on information in NMFS (2022c). Its distribution is largely restricted to the Coral Triangle and parts of the western equatorial Pacific Ocean, which is projected to have the most rapid and severe impacts from climate change and localized human impacts for coral reefs over the 21st century. The current information indicates that *A. tenella* occurs in five more MEOWs than we were aware of at the time of listing in 2014, including the Solomon Islands, Coral Sea, New Caledonia, East China Sea and South Kuroshio MEOWs (NMFS 2022c). These new records extend long distances both northwards and southeastwards, indicating that the species' geographic distribution is considerably larger than previously known.

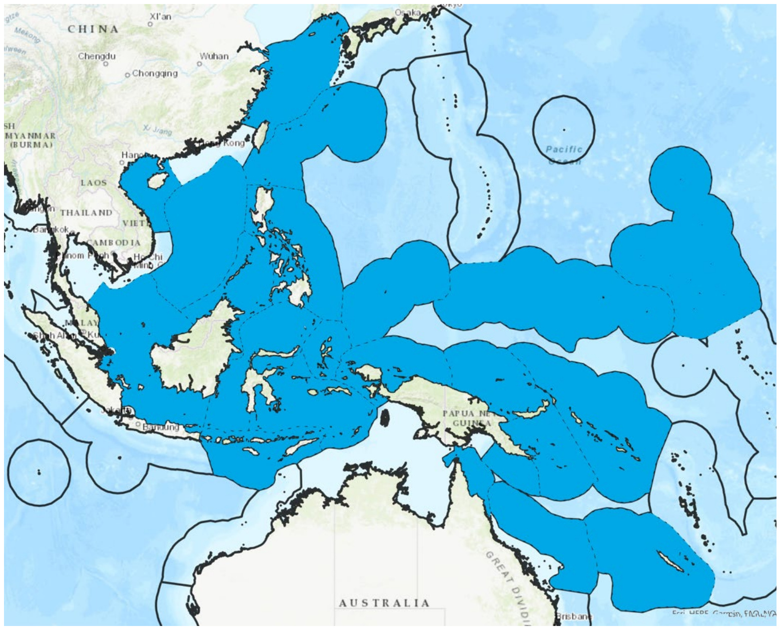


Figure 20. Geographic distribution of *A. tenella*.

Depth Distribution. The species inhabits an extraordinary range of depths, but most commonly occurs at >40 m (Turak and Devantier 2019, Muir et al. 2019). However, it sometimes occurs much shallower, and has been reported at 6 m (Irian Jaya, Muir et al. 2019), 13 m (Pohnpei, Muir and Wallace 2016), 15 m (Bismark Sea; Turak and Devantier 2019), 18 m (Rowley et al. 2019), and 22 m (Palau, Pat Colin, personal communication 2020). Mesophotic surveys found *A. tenella* at 25 to 110 m (Muir et al. 2019). Thus, current information indicates that *A. tenella* has a far broader depth range (6–110 m), including both much shallower and much deeper than we were aware of at the time of listing in 2014 (40–70 m).

Relevance of Distribution to Status. Geographic and depth distributions were the key spatial factors considered in determining the status of coral species and in the listing of *A. tenella* in 2014. A narrow geographic or depth distribution exacerbates a species' extinction risk because larger proportions of the population are likely to be exposed to any single disturbance. In contrast, a broad overall distribution moderates a species' extinction risk because the population is distributed across a range of geographic areas and depths, and thus lower proportions of the populations are likely to be exposed to any single disturbance. For example, one reason that *A. tenella* was listed was because the information available at that time indicated a geographic distribution restricted mainly to the Coral Triangle (79 FR 53851). Since both the geographic and depth distributions of *A. tenella* are greater than we were aware of at the time of listing in 2014, its distribution has a greater capacity to moderate extinction risk.

4.8.3. Abundance

Relative Abundance: DeVantier and Turak (2017) characterized abundances of over 600 Indo-Pacific reef-building coral species in 31 Veron ecoregions from the Red Sea to Fiji, as further described in Section 4.1.3 above. *Acropora tenella* was recorded in 9 of the 31 ecoregions. Within those 9 ecoregions, it had a mean overall abundance of 2.70 (Uncommon), ranging from 0.95 (Rare) in the Raja Ampat, Papua Ecoregion to 6.25 (Uncommon) in the GBR Far North and Torres Strait Ecoregion. The mean overall abundance of *A. tenella* for all 31 ecoregions was 0.72 (Rare, DeVantier and Turak 2017, Table S2), however some of the 22 ecoregions where it was not recorded may be outside its range. Another consideration is that *A. tenella* occurs primarily in the upper mesophotic zone (30–50 m), and the surveys were conducted mostly at <40 m (DeVantier and Turak 2017). The Coral Traits Database (https://coraltraits.org/, accessed August 2022) lists *A. tenella*'s global relative abundance as "uncommon," but does not cite DeVantier and Turak (2017).

More recent information from mesophotic surveys (>30 m) report that *A. tenella* is common at some locations and depths. In surveys of the upper mesophotic zone in southern Japan, *A. tenella* was the fourth-most abundant species, forming extensive, dense patches of unattached branches over rubble and sand (Sinniger et al. 2019). Other studies also indicate that *A. tenella* is common in the upper mesophotic zone in southern Japan (Prasetia et al. 2016, Sinniger et al. 2012). Likewise, *A. tenella* is reported as one of the most common upper mesophotic corals over rubble and sand in Taiwan (Denis et al. 2019). In Palau, *A. tenella* is reported as the most common *Acropora* species below 30 m (Colin and Lindfield 2019). In Kimbe Bay, Papua New Guinea, the upper mesophotic coral community features extensive coverage of *A. tenella* (Longenecker et al. 2019, Turak and DeVantier 2019). In the upper mesophotic zone in the Coral Sea, *A. tenella* forms extensive monospecific stands comparable in size to those of staghorn corals in shallow-reef habitats (Muir et al. 2015, Bridge et al. 2019, Pinheiro et al. 2019). A mesophotic coral survey at 25–110 m depth in the Coral Sea found *A. tenella* at 5 of the 28 sites, where it formed large colonies with distinctive, long branches (Muir et al. 2019). Within its range, the relative abundance of *A. tenella* may vary locally from very rare to at least common at mesophotic depths. However, based on the above information, the rangewide relative abundance of *A. tenella* is uncommon to common. Thus, current information indicates that *A. tenella* has a higher relative abundance (uncommon to common) than we were aware of at the time of listing in 2014 (rare).

Absolute Abundance. Absolute abundance is an estimate of the total number of colonies of a species that currently exist throughout its range. Based on information from Richards et al. (2008, 2019), *A. tenella* had a population estimate of 5,207,000 colonies, and an effective population size of 573,000 colonies (79 FR 53851). However, since then we have learned that the species has a broader geographic distribution, a much broader depth distribution, and higher relative abundance. Based on the updated information, *A. tenella*'s absolute abundance is likely to be at least tens of millions of colonies. Thus, current information indicates that *A. tenella* has a higher absolute abundance (at least tens of millions) than we were aware of at the time of listing in 2014 (approximately 5.2 million).

Abundance Trends. As described above in the general Threats Evaluation and below for threats to *A. tenella*, the most important threats (i.e., ocean warming, ocean acidification) have worsened since 2014, and substantial impacts to *Acropora* species have occurred, although no species-specific data are available for *A. tenella*. Based on the continued worsening in the most important threats, it is likely that *A. tenella* is decreasing in overall abundance (i.e., abundance across all the ecoregions that make up its range).

Relevance of Abundance to Status. Abundance is the key demographic factor considered in determining the status of coral species and in the listing of *A. tenella* in 2014. A low relative or absolute abundance, especially in combination with declining abundance, exacerbates a species' extinction risk because larger proportions of the population are likely to be exposed to any single disturbance. In contrast, a higher relative or absolute abundance moderates a species' extinction risk because lower proportions of the population are likely to be exposed to any single disturbance (79 FR 53851). Since the relative abundance and absolute abundance of *A. tenella* are both greater than we were aware of in at the time of listing in 2014, its abundance may have a greater capacity to moderate extinction risk.

4.8.4. Threats

This section provides an updated threats evaluation for *A. tenella*, focusing on the threats that contributed to its listing (79 FR 53851), including ocean warming, ocean acidification, disease, fishing, LBSP, predation, and inadequacy of existing regulatory mechanisms. In addition, current information indicates that collection and trade is also impacting the status of the species. A threats summary table is provided, including relative importance ratings for the threats, effects of threats since listing in 2014, and projected effects of threats in the foreseeable future.

Ocean Warming: As noted in Section 3.2.1 above, since listing in 2014, the effects of ocean warming on Indo-Pacific reef-building corals in general have substantially worsened. In response to the 2014–2017 series of warming-induced bleaching events, *Acropora* corals were generally the most impacted coral taxa in different locations around the Indo-Pacific (e.g., Hoogenboom et al. 2017, Frade et al 2018, Hughes et al. 2018a,b, Raymundo et al. 2019, Thinesh et al. 2019, Dietzel et al. 2020, Gilmour et al. 2022). Section 3.2.1 also describes how ocean warming is projected to greatly worsen in the foreseeable future (i.e., between now and 2100). In conclusion, the current information indicates that *A. tenella* continues to be highly susceptible to ocean warming, that this threat has substantially worsened since listing in 2014, and that it will greatly worsen in the foreseeable future (Table 11).

Ocean Acidification: As noted in Section 3.2.2 above, since listing in 2014, the effects of ocean acidification on Indo-Pacific reef-building corals have worsened. Generally, *Acropora* species are susceptible to reduced calcification and skeletal growth from ocean acidification (Brainard et al. 2011, 79 FR 53851, Smith et al. 2020, Evenson et al. 2021, Hill and Hoogenboom 2022). Section 3.2.2 also describes how ocean acidification is projected to greatly worsen in the foreseeable future. In conclusion, the current information indicates that *A. tenella* continues to be susceptible to ocean acidification, that this threat has worsened since listing in 2014, and that it will greatly worsen in the foreseeable future (Table 11).

Disease: As noted in Section 3.2.3 above, since listing in 2014, the effects of disease on Indo-Pacific corals have increased, mainly in response to the 2014–2017 bleaching events. Generally, *Acropora* species are susceptible to most of the diseases that infect coral, and are more commonly affected by acute and lethal diseases than other corals (Brainard et al. 2011, 79 FR 53851, Hobbs et al. 2015, Aeby et al. 2020, Howells et al. 2020). Section 3.2.3 also describes how disease is projected to substantially worsen in the foreseeable future. In conclusion, the current information indicates that *A. tenella* continues to be susceptible to disease, that this threat has worsened since listing in 2014, and that it will substantially worsen in the foreseeable future (Table 11).

Fishing: As noted in Section 3.2.4 above, since listing in 2014, the direct and indirect effects of fishing on Indo-Pacific corals have continued, likely intensifying in some locations while lessening in others due to various factors. Generally, branching, fast-growing corals such as most *Acropora* species are susceptible to direct (i.e., damage by fishing gear because of their morphology) and indirect (i.e., increased competition for space with algae) effects of fishing (Brainard et al. 2011, 79 FR 53851). Section 3.2.4 also describes how fishing is projected to substantially worsen in the foreseeable future. In conclusion, the current information indicates that *A. tenella* continues to be susceptible to fishing, that this threat has continued since listing in 2014, and that it will substantially worsen in the foreseeable future (Table 11).

LBSP: As noted in Section 3.2.5 above, since listing in 2014, the effects of LBSP on Indo-Pacific corals have continued, likely intensifying in some locations while lessening in others due to various factors. Generally, *Acropora* species are relatively susceptible to sediment and nutrients compared to other reef-building coral taxa (Brainard et al. 2011, 79 FR 53851, Carlson et al. 2019, Tuttle and Donahue 2022). Section 3.2.5 also describes how LBSP is projected to substantially worsen in the foreseeable future. In conclusion, the current information indicates that *A. tenella* continues to be susceptible to LBSP, that this threat has continued since listing in 2014, and that it will substantially worsen in the foreseeable future (Table 11).

Predation: As noted in Section 3.2.6 above, since listing in 2014, the effects of predation on Indo-Pacific corals have increased, mainly because the 2014–2017 bleaching events resulted in more favorable conditions for predators such as COTS. Generally, *Acropora* species are relatively susceptible to predation compared to other reef-building coral taxa (Brainard et al. 2011, 79 FR 53851, Keesing et al. 2019, Tkachenko and Huang 2022). Section 3.2.6 also describes how predation is projected to substantially worsen in the foreseeable future. In conclusion, the current information indicates that *A. tenella* continues to be susceptible to predation, that this threat has worsened since listing in 2014, and that it will substantially worsen in the foreseeable future (Table 11).

Collection and Trade: Although collection and trade did not contribute to the listing of *A. tenella* (79 FR 53851), the following information indicates that this threat is likely impacting the status of the species. As noted in Section 3.2.7 above, since listing in 2014, the effects of collection and trade on Indo-Pacific corals have continued. According to the CITES database cited in Section 3.2.7, between 1985 and 2017, over 17 million *Acropora* units were globally imported and exported. These units were not identified to species, thus likely included an undeterminable number of unidentified *A. tenella*. In addition, the database also records that between 2011 and 2017, dozens of *A. tenella* units were globally imported and exported most years (NMFS 2022a). Because of the popularity of *A. tenella* in the marine aquarium trade (Adams 2014) as well as the ongoing and projected growth in the industry, collection and trade may increasingly impact the status of *A. tenella*. Section 3.2.7 also describes how collection and trade is projected to substantially worsen in the foreseeable future. In conclusion, the current information indicates that *A. tenella* is susceptible to collection and trade, that this threat has continued since listing in 2014, and that it will substantially worsen in the foreseeable future (Table 11).

Sea-level Rise: As noted in Section 3.2.8 above, since listing in 2014, sea-level rise has likely been too gradual to result in measurable effects on Indo-Pacific reef-building corals. In those cases where earthquakes have resulted in substrate uplift resembling sea-level rise, these substrates have been colonized by rapidly-growing corals like *Acropora* species. In conclusion, as in the final rule, the current information indicates that *A. tenella* is not susceptible to sea-level rise, that there have been no detectable trends in the effects of this threat since listing in 2014, but that it will worsen in the foreseeable future (Table 11).

Regulatory Mechanisms: As noted in Section 3.2.9 above, since listing in 2014, some progress has been made with GHG management as well as controlling local threats although existing regulatory mechanisms are still inadequate to control any of the threats. Section 3.2.9 also describes how it is unlikely that regulatory mechanisms will be improved to the point where they are adequate to control any of the threats in the foreseeable future. In conclusion, the current information indicates that existing regulatory mechanisms remain inadequate to control any threat to *A. tenella*, and that improvement is unlikely in the foreseeable future (Table 11).

Threats Conclusion for *A. tenella*: Since *A. tenella* was listed in 2014, many of the threats to the species have worsened. Especially concerning is that the most important threat to the species, ocean warming, has substantially worsened. In addition, all threats are projected to worsen in the foreseeable future, with the possible exception of regulatory mechanisms, which may continue to improve but also are likely to remain inadequate for controlling any of the threats (Table 11).

Although the final rule rated the relative importance of threats to the world's reef-building corals (Table 2), it did not apply those ratings to *A. tenella* (79 FR 53851). Instead, the final rule concluded that *A. tenella* is highly susceptible to ocean warming and susceptible to ocean acidification, disease, fishing, LBSP, and predation, while regulatory mechanisms were inadequate for controlling any threat (79 FR 53851). However, as summarized above, we now have more genus-specific and species-specific information available on the importance of each threat to *Acropora* species and *A. tenella*, respectively. Based on the general importance ratings of the threats to Indo-Pacific reef-building corals (Table 3) and the genus-specific and species-specific information above, we conclude that the relative importance ratings of each threat to Indo-Pacific corals apply to *A. tenella*. In addition, the observed threat trends since 2014 and projected threat trends in the foreseeable future are provided (Table 11).

Table 11. Summary of threats evaluation for *A. tenella*. For each threat, relative importance to the extinction risk of the species, observed trend since 2014, and projected trend in the foreseeable future are provided.

Threat (listing factor)	**Importance**	**Observed Trend in Effects Since 2014**	**Projected Trend in Effects to 2100**
Ocean Warming (Factor E)	Very High	Substantially worsened	Greatly worsen
Ocean Acidification (Factor E)	High	Worsened	Greatly worsen
Disease (Factor C)	High	Worsened	Substantially worsen
Fishing (Factor A)	Medium	Continued	Substantially worsen
LBSP (Factors A and E)	Low-Medium	Continued	Substantially worsen
Predation (Factor C)	Low-Medium	Worsened	Substantially worsen
Collection and Trade (Factor B)	Low-Medium	Continued	Substantially worsen
Sea-level Rise (Factor E)	Low	No detectable trends	Worsen
Inadequacy of Existing Regulatory Mechanisms (Factor D)	High	Some improvement but still inadequate	Improvement but likely still inadequate

4.8.5. Conclusion

As explained in the 2014 final listing rule (79 FR 53851), a species' vulnerability to extinction results from the combination of its spatial (i.e., distribution) and demographic (i.e., abundance) characteristics, threat susceptibilities, and consideration of the baseline environment and future projections of threats. *Acropora tenella* was listed as threatened in 2014 because of its limited geographic distribution, low abundance, high susceptibility to ocean warming, susceptibilities to ocean acidification, fishing, LBSP, disease, and predation, inadequate regulatory mechanisms, declining baseline conditions, and projected worsening of threats (79 FR 53851).

Since 2014, we have learned that *A. tenella* has: (1) a broader geographic distribution (23 MEOWs instead of 18); (2) a much broader depth range (6–110 m instead of 40–70 m); (3) higher relative abundance (uncommon to common instead of rare); and (4) higher absolute abundance (at least tens of millions of colonies instead of approximately 5.2 million colonies) than we believed in 2014. That is, *A. tenella* is more broadly distributed and more abundant than we believed in 2014, and thus may have a higher capacity to moderate the effects of the threats, as explained in the Relevance of Distribution/Abundance to Status sections above.

Since 2014, the effects of ocean warming have substantially worsened, and the effects of most other threats have worsened as well. All threats are projected to substantially worsen under current global GHG regulatory mechanisms, which would result in global warming of 2.6–3.4°C above the pre-industrial baseline by 2100 (see Fig. 4 in Section 3.1 above). Even if the goal of the Paris Agreement is achieved (i.e., limiting global warming to 1.5°C above pre-industrial by 2100), the threats would become much worse than they are currently (Dixon et al. 2022), likely preventing the recovery of *A. tenella*. Current regulatory mechanisms are grossly inadequate, especially GHG management.

In conclusion, the above information shows that *A. tenella* is more broadly distributed and more abundant than we believed in 2014, but that the threats have worsened and that collection and trade is also an important threat to the species. Especially concerning is that the most important threat to the species, ocean warming, has substantially worsened since the species was listed in 2014. The other important threats to the species, including ocean acidification,disease, fishing, LBSP, predation, and collection and trade have also either worsened or continued since 2014. While there has been some progress with regulatory mechanisms, primarily because of the 2016 Paris Agreement, regulatory mechanisms for both global and local threats are still inadequate. However, the species' distribution is broader and its abundance is greater than we were aware of at the time of listing in 2014, both of which are key factors for moderating threats.

4.9. *Anacropora spinosa* (Rehberg 1892)

4.9.1. Biology

Taxonomy. This species was described by Rehberg (1892). It is included in the Corals of the World books (Veron 2000) and website (http://www.coralsoftheworld.org/, accessed August 2022), and is accepted by WoRMS (Hoeksma and Cairns 2021).

Morphology. Colonies of *A. spinosa* have thin, upward growing cylindrical branches. Branches are delicate and usually form thickets by fragmentation. Branch tips are relatively sharp and smooth because they do not have a corallite at the end of the branch, a characteristic of the genus *Anacropora*. Branches have many spines along their sides, which may taper and may be variable in size. Colonies are pale brown in color, occasionally with white tips (Fig. 21, Veron 2000, Veron et al. 2016).

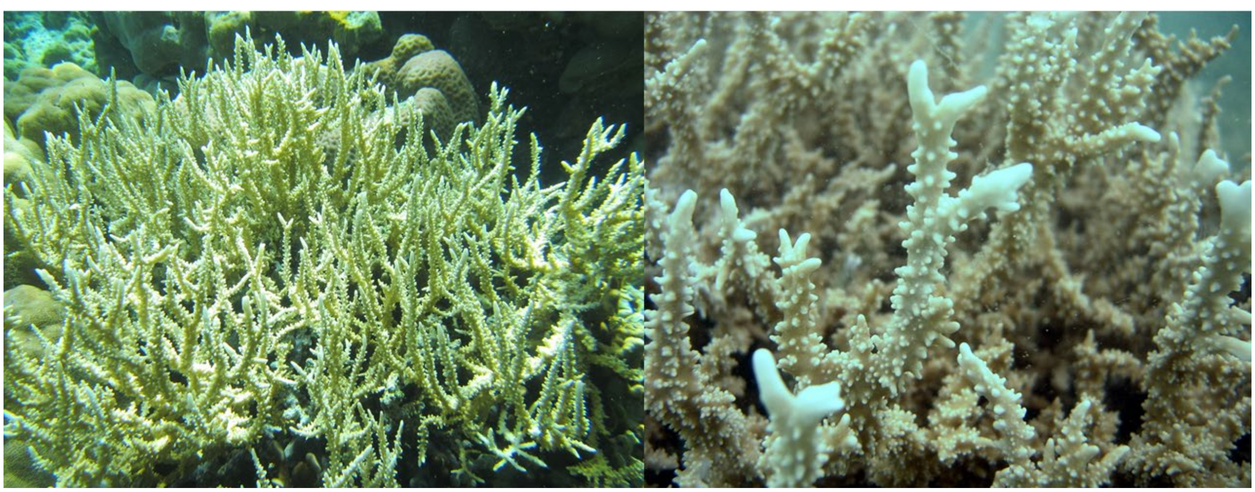


Figure 21. *Anacropora spinosa*, showing colony and branch morphology. Colony photo is from Palau, and branch photo is from New Caledonia (photos copyright, Doug Fenner).

Habitat. The Coral Traits Database (https://coraltraits.org/, accessed August 2022) lists *A. spinosa*'s water clarity preference as "clear," and wave exposure preference as "broad." However, it also occurs in turbid water, and is found on sand and mud as well as hard substrates (Doug Fenner, personal communication 2020).

Life History. Little information is available on the life history of *A. speciosa*. Generally, *Anacropora* species have rapid skeletal growth and low tolerance to thermal stress, and all are hermaphroditic broadcast spawners (Brainard et al. 2011). Asexual reproduction via branch fragmentation is common in this species, commonly producing small to large thickets (Doug Fenner, personal communication 2020). Many *Anacropora* species are adapted to turbidity and sediment by having widely-spaced thin branches that allow sediment to fall through the colonies, which grow upwards at rates sufficient to avoid burial. Excavation of bases of such colonies can reveal a deep network of sediment-buried branches (Turak and DeVantier 2019).

4.9.2. Distribution

Geographic Distribution. *Anacropora spinosa* has a relatively limited distribution, occurring in 17 MEOWs (Fig. 22), and does not occur in U.S. waters based on information in NMFS (2022c). Its distribution is largely restricted to the Coral Triangle region, which is projected to have the most rapid and severe impacts from climate change and localized human impacts for coral reefs over the 21st century. The current information indicates that *A. spinosa* occurs in one more MEOW (New Caledonia) than we were aware of at the time of listing in 2014 (NMFS 2022c), considerably extending the geographic distribution of the species to the southeast.

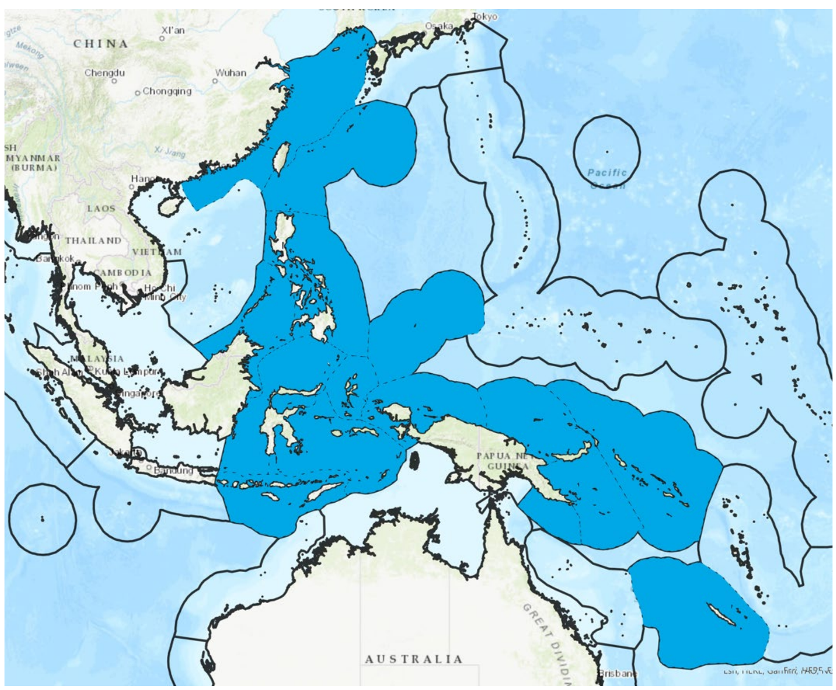


Figure 22. Geographic distribution of *A. spinosa*.

Depth Distribution. *Acropora spinosa* occurs at 5-15 m of depth (Coral Traits Database https://coraltraits.org/, accessed August 2022), the same depth distribution as reported in the 2014 final listing rule.

Relevance of Distribution to Status. Geographic and depth distributions were the key spatial factors considered in determining the status of coral species and in the listing of *A. spinosa* in 2014. A narrow geographic or depth distribution exacerbates a species' extinction risk because larger proportions of the population are likely to be exposed to any single disturbance.In contrast, a broad overall distribution moderates a species' extinction risk because the population is distributed across a range of geographic areas and depths, and thus lower proportions of the populations are likely to be exposed to any single disturbance. For example, one reason that *A. spinosa* was listed was because of its narrow depth distribution of 5–15 m (79 FR 53851).

4.9.3. Abundance

Relative Abundance: DeVantier and Turak (2017) characterized abundances of over 600 Indo-Pacific reef-building coral species in 31 Veron ecoregions from the Red Sea to Fiji, as further described in Section 4.1.3 above. *Anacropora spinosa* was recorded in 9 of the 31 ecoregions. Within those 9 ecoregions, it had a mean overall abundance of 8.97 (Uncommon), ranging from 2.50 (Uncommon) in the Celebes Sea Ecoregion to 18.18 (Common) in the Cenderawasih Bay, Papua Ecoregion. The mean overall abundance of *A. spinosa* for all 31 ecoregions was 2.63 (Uncommon, DeVantier and Turak 2017, Table S2), however some of the 22 ecoregions where it was not recorded may be outside its range. The Coral Traits Database (https://coraltraits.org/, accessed August 2022) lists *A. spinosa*'s global relative abundance as "uncommon", but does not cite DeVantier and Turak (2017). Within its range, the relative abundance of *A. spinosa* may vary locally from very rare to at least common. However, based on the above information, the rangewide relative abundance of *A. spinosa* is uncommon.

Absolute Abundance. Absolute abundance is an estimate of the total number of colonies of a species that currently exist throughout its range. Based on *A. spinosa's* distribution and relative abundance, NMFS (2014) estimated the absolute abundance of *A. spinosa* be at least millions of colonies. Based on current information, no changes to that estimate are warranted.

Abundance Trends. As described above in the general Threats Evaluation and below for threats to *A. spinosa*, the most important threat (i.e., ocean warming) has worsened since 2014, and substantial impacts to *Anacropora* species have occurred, although no species-specific data are available for *A. spinosa*. Based on the continued worsening in the most important threats, it is likely that *A. spinosa* is decreasing in overall abundance (i.e., abundance across all the ecoregions that make up its range).

Relevance of Abundance to Status. Abundance is the key demographic factor considered in determining the status of coral species and in the listing of *A. spinosa* in 2014. A low relative or absolute abundance, especially in combination with declining abundance, exacerbates a species' extinction risk because larger proportions of the population are likely to be exposed to any single disturbance. In contrast, a higher relative or absolute abundance moderates a species' extinction risk because lower proportions of the population are likely to be exposed to any single disturbance (79 FR 53851).

4.9.4. Threats

This section provides an updated threats evaluation for *A. spinosa*, focusing on the threats that contributed to its listing (79 FR 53851), which included ocean warming, ocean acidification, disease, fishing, LBSP, predation, and inadequacy of existing regulatory mechanisms. In addition, current information indicates that collection and trade is also impacting the status of the species. A threats summary table is provided, including relative importance ratings for the threats, effects of threats since listing in 2014, and projected effects of threats in the foreseeable future.

Ocean Warming: As noted in Section 3.2.1 above, since listing in 2014, the effects of ocean warming on Indo-Pacific reef-building corals in general have substantially worsened. In response to warming events in 2016 and 2020, *Anacropora* corals were among the most susceptible to bleaching of all corals (Muir et al. 2017, Nolan et al. 2021). Section 3.2.1 also describes how ocean warming is projected to greatly worsen in the foreseeable future (i.e., between now and 2100). In conclusion, the current information indicates that *A. spinosa* continues to be susceptible to ocean warming, that this threat has substantially worsened since listing in 2014, and that it will greatly worsen in the foreseeable future (Table 12).

Ocean Acidification: As noted in Section 3.2.2 above, since listing in 2014, the effects of ocean acidification on Indo-Pacific reef-building corals have worsened. While new information since the 2014 listing indicates that some *Anacropora* corals occur in naturally low pH environments (Barkley et al. 2015, van Woesik and Cacciapaglia 2018, Maggioni et al. 2021), whether that means *A. spinosa* generally has low susceptibility to ocean acidification is unknown. Section 3.2.2 also describes how ocean acidification is projected to greatly worsen in the foreseeable future. In conclusion, while the current information indicates potentially lower susceptibility of *A. spinosa* to ocean acidification, there is no species-specific information. Thus we still conclude that the species is susceptible to this threat. Furthermore, ocean acidification has worsened since listing in 2014, and it is likely to greatly worsen in the foreseeable future (Table 12).

Disease: As noted in Section 3.2.3 above, since listing in 2014, the effects of disease on Indo-Pacific corals have increased, mainly in response to the 2014–2017 bleaching events. The little information available on disease in *Anacropora* species indicates some susceptibility (79 FR 53851). Section 3.2.3 also describes how disease is projected to substantially worsen in the foreseeable future. In conclusion, the current information indicates that *A. spinosa* continues to be susceptible to disease, that this threat has worsened since listing in 2014, and that it will substantially worsen in the foreseeable future (Table 12).

Fishing: As noted in Section 3.2.4 above, since listing in 2014, the direct and indirect effects of fishing on Indo-Pacific corals have continued, likely intensifying in some locations while lessening in others due to various factors. Generally, branching corals such as most *Anacropora* species may be more susceptible than other corals to damage by fishing gear because of their morphology (Brainard et al. 2011, 79 FR 53851). Section 3.2.4 also describes how fishing is projected to substantially worsen in the foreseeable future. In conclusion, the current information indicates that *A. spinosa* continues to be susceptible to fishing, that this threat has continued since listing in 2014, and that it will substantially worsen in the foreseeable future (Table 12).

LBSP: As noted in Section 3.2.5 above, since listing in 2014, the effects of LBSP on Indo-Pacific corals have continued, likely intensifying in some locations while lessening in others due to various factors. While new information since the 2014 listing indicates that some *Anacropora* corals are adapted to turbidity and sediment (Turak and DeVantier 2019), whether that means *A. spinosa* generally has low susceptibility to LBSP is unknown. In conclusion, while the current information indicates potentially lower susceptibility of *A. spinosa* to LBSP, there is no species-specific information. Thus we still conclude that the species is susceptible to this threat. Furthermore, LBSP has worsened since listing in 2014, and it is likely to substantially worsen in the foreseeable future (Table 12).

Predation: As noted in Section 3.2.6 above, since listing in 2014, the effects of predation on Indo-Pacific corals have increased, mainly because the 2014–2017 bleaching events resulted in more favorable conditions for predators such as COTS. The little information available on predation of *Anacropora* species indicates some susceptibility (79 FR 53851). Section 3.2.6 also describes how predation is projected to substantially worsen in the foreseeable future. In conclusion, the current information indicates that *A. spinosa* continues to be susceptible to predation, that this threat has worsened since listing in 2014, and that it will substantially worsen in the foreseeable future (Table 12).

Collection and Trade: Although collection and trade did not contribute to the listing of *A. spinosa* (79 FR 53851), the following information indicates that this threat is likely impacting the status of the species. As noted in Section 3.2.7 above, since listing in 2014, the effects of collection and trade on Indo-Pacific corals have continued. According to the CITES database cited in Section 3.2.7, between 2011 and 2016, several hundred *Anacropora* units were globally imported and exported. These units were not identified to species, thus likely included an undeterminable number of unidentified *A. spinosa*. In addition, the database also records that 10 *A. spinosa* units were globally imported and exported in 2009 (NMFS 2022a). Because of the growing popularity of *Anacropora* coral in the marine aquarium trade (Adams 2022) as well as the ongoing and projected growth in the industry, collection and trade may increasingly impact the status of *A. spinosa*. Section 3.2.7 also describes how collection and trade is projected to substantially worsen in the foreseeable future. In conclusion, the current information indicates that *A. spinosa* is susceptible to collection and trade, that this threat has continued since listing in 2014, and that it will substantially worsen in the foreseeable future (Table 12).

Sea-level Rise: As noted in Section 3.2.8 above, since listing in 2014, sea-level rise has likely been too gradual to result in measurable effects on Indo-Pacific reef-building corals. In those cases where earthquakes have resulted in substrate uplift resembling sea-level rise, these substrates have been colonized by rapidly-growing corals like *Anacropora* species. In conclusion, as in the final rule, the current information indicates that *A. spinosa* is not susceptible to sea-level rise, that there have been no detectable trends in the effects of this threat since listing in 2014, but that it will worsen in the foreseeable future (Table 12).

Regulatory Mechanisms: As noted in Section 3.2.9 above, since listing in 2014, some progress has been made with GHG management as well as controlling local threats although existing regulatory mechanisms are still inadequate to control any of the threats. Section 3.2.9 also describes how it is unlikely that regulatory mechanisms will be improved to the point where they are adequate to control any of the threats in the foreseeable future. In conclusion, the current information indicates that existing regulatory mechanisms remain inadequate to control any threat to *A. spinosa*, and that improvement is unlikely in the foreseeable future (Table 12).

Threats Conclusion for *A. spinosa*: Since *A. spinosa* was listed in 2014, many of the threats to the species have worsened. All threats are projected to worsen in the foreseeable future, with the possible exception of regulatory mechanisms, which may continue to improve but also are likely to remain inadequate for controlling any of the threats (Table 12).

Although the final rule rated the relative importance of threats to the world's reef-building corals (Table 2), it did not apply those ratings to *A. spinosa* (79 FR 53851). Instead, the final rule concluded that *A. spinosa* is susceptible to ocean warming, ocean acidification, disease, fishing, LBSP, and predation, while regulatory mechanisms were inadequate for controlling any threat (79 FR 53851). However, as summarized above, we now have more genus-specific and species-specific information available on the importance of each threat to *Anacropora* species and *A. spinosa*, respectively. Based on the general importance ratings of the threats to Indo-Pacific reef-building corals (Table 3) and the genus-specific and species-specific information above, we conclude that the relative importance ratings of each threat to Indo-Pacific corals apply to *A. spinosa*. In addition, the observed threat trends since 2014 and projected threat trends in the foreseeable future are provided (Table 12).

Table 12. Summary of threats evaluation for *A. spinosa*. For each threat, relative importance to the extinction risk of the species, observed trend since 2014, and projected trend in the foreseeable future are provided.

Threat (listing factor)	Importance	Observed Trend in Effects Since 2014	Projected Trend in Effects to 2100
Ocean Warming (Factor E)	Very High	Substantially worsened	Greatly worsen
Ocean Acidification (Factor E)	High	Worsened	Greatly worsen
Disease (Factor C)	High	Worsened	Substantially worsen
Fishing (Factor A)	Medium	Continued	Substantially worsen
LBSP (Factors A and E)	Low-Medium	Continued	Substantially worsen
Predation (Factor C)	Low-Medium	Worsened	Substantially worsen
Collection and Trade (Factor B)	Low-Medium	Continued	Substantially worsen
Sea-level Rise (Factor E)	Low	No detectable trends	Worsen
Inadequacy of Existing Regulatory Mechanisms (Factor D)	High	Some improvement but still inadequate	Improvement but likely still inadequate

4.9.5. Conclusion

As explained in the 2014 final listing rule (79 FR 53851), a species' vulnerability to extinction results from the combination of its spatial (i.e., distribution) and demographic (i.e., abundance) characteristics, threat susceptibilities, and consideration of the baseline environment and future projections of threats. *Anacropora spinosa* was listed as threatened in 2014 because of its limited geographic distribution largely restricted to the Coral Triangle region, susceptibilities to ocean warming, ocean acidification, fishing, LBSP, disease, and predation, inadequate regulatory mechanisms, declining baseline conditions, and projected worsening of threats (79 FR 53851).

Since 2014, we have learned that *A. spinosa* has a broader geographic distribution (17 MEOWs instead of 16) than reported in the 2014 final listing rule. While its geographic distribution is only one MEOW greater, the addition of that MEOW (New Caledonia) means that its geographic distribution extends much farther to the southeast and includes over 100 more islands and extensive coral reefs than previously believed. That is, *A. spinosa* is more broadly distributed than we believed in 2014, and thus may have a higher capacity to moderate the effects of the threats, as explained in the Relevance of Distribution to Status section above.

Since 2014, the effects of ocean warming have substantially worsened, and the effects of most other threats have worsened as well. All threats are projected to substantially worsen under current global GHG regulatory mechanisms, which would result in global warming of 2.6–3.4°C above the pre-industrial baseline by 2100 (see Fig. 4 in Section 3.1 above). Even if the goal of the Paris Agreement is achieved (i.e., limiting global warming to 1.5°C above pre-industrial by 2100), the threats would become much worse than they are currently (Dixon et al. 2022), likely preventing the recovery of *A. spinosa*. Current regulatory mechanisms are grossly inadequate, especially GHG management.

In conclusion, the above information shows that *A. spinosa* is more broadly distributed than we believed in 2014, but that the threats have worsened and that collection and trade is also an important threat to the species. Especially concerning is that the most important threat to the species, ocean warming, has substantially worsened since the species was listed in 2014. The other important threats to the species, including ocean acidification,disease, fishing, LBSP, predation, and collection and trade have also either worsened or continued since 2014. While there has been some progress with regulatory mechanisms, primarily because of the 2016 Paris Agreement, regulatory mechanisms for both global and local threats are still inadequate. However, the species' distribution is broader than we were aware of at the time of listing in 2014, which is a key factor for moderating threats.

4.10. *Fimbriaphyllia paradivisa* (Veron 1990)

4.10.1. Biology

Taxonomy. This species was listed as *Euphyllia paradivisa* in 2014 (79 FR 53851). Since then, Luzon et al. (2017) elevated *Fimbriaphyllia* from a subgenus to replace the *Euphyllia* genus, based on genetics results, thus changing *Euphyllia paradivisa* to *Fimbriaphyllia paradivisa*, which is accepted by WoRMS (Hoeksma and Cairns 2021). We now use the WoRMS-accepted name of *Fimbriaphyllia paradivisa*. Historically, Veron and Pichon (1980) divided the genus *Euphyllia* into two subgenera, *Euphyllia* and *Fimbriaphyllia*, based on skeletal characteristics. Veron (1990) described the species as *Euphyllia paradivisa* but that name is no longer accepted by WoRMS (Hoeksma and Cairns 2021).

Morphology. Colonies of *F. paradivisa* consist of branching, separate corallites. Like all *Fimbriaphyllia* species, *F. paradivisa* has large polyps with tentacles that can be extended 10–20 cm (Eyal et al. 2016). Polyps have branching tentacles, an important characteristic for distinguishing it from other *Fimbriaphyllia* species. Color is typically pale greenish-grey with lighter tentacle tips (Fig. 23, Fenner and Burdick 2016, Veron et al. 2016, Fenner 2020a).

Figure 23. *Fimbriaphyllia paradivisa*, showing corallite skeleton, and a colony with tentacles extended. Both photos are of Philippines' corals (Charlie Veron; Veron et al. 2016).

Habitat. *Fimbriaphyllia paradivisa* occurs mainly in low light environments protected from wave action across a wide depth range, such as shallow turbid bays (Fujii et al. 2020) and mesophotic depths (Eyal et al. 2016). It is also sometimes found on shallow reefs in clear water (Turak and DeVantier 2019). Colonies of *F. paradivisa* have been reported from a variety of substrates, including mud (Fenner 2020a, Fujii et al. 2020), sand and rubble (Fenner 2001, Loya et al. 2016, Sinniger and Harii 2018), and rock (Toonen and Montgomery 2018, Montgomery et al. 2019, NMFS 2022b).

Life History. Generally, *Fimbriaphyllia* species are slow-growing and stress-tolerant (Morgan et al. 2016, Zweifler et al. 2021). *Fimbriaphyllia paradivisa* is a broadcast spawner, whereby both male and female gametes are released into the water column and fertilization takes place externally. Colonies are gonochoric, in that separate colonies produce eggs and sperm (Luzon et al. 2017). Like other *Fimbriaphyllia* species, *F. paradivisa* has large polyps with tentacles that can be extended 10–20 cm, enhancing its capacity for feeding on plankton. In 2016, a large mesophotic population of *F. paradivisa* was reported from the northern Red Sea, leading to extensive field and laboratory work (e.g., Eyal et al. 2016, Ben-Zvi et al. 2019, Eyal et al. 2019, Tamir et al. 2019, Ben-Zvi et al. 2020, Meron et al. 2020, Rinsky et al. 2022). These studies provide new information on the life history of this population of *F. paradivisa*, including that it is highly competitive for space (Eyal et al. 2016), has high physiological plasticity as shown by its ability to survive for extended periods of time with no zooxanthellae and other characteristics (Eyal et al. 2016, Rinsky et al. 2022), displays dramatic color polymorphism as a result of its intense fluorescence (Ben-Zvi et al. 2019), has high photoacclimation capacity (Eyal et al. 2019, Ben-Zvi et al. 2020), and does not occur shallower than 40 m or deeper than 80 m, but is the dominant coral species at 40–70 m (Tamir et al. 2019).

4.10.2. Distribution

Geographic Distribution. *Fimbriaphyllia paradivisa* occurs in 24 MEOWs (Fig. 24) including within U.S. waters, based on information in NMFS (2022c). The current information indicates that *F. paradivisa* occurs in nine more MEOWs than we were aware of at the time of listing in 2014 (NMFS 2022c), including the Red Sea, Gulf of Aden, Southern China, East China Sea, South Kuroshio, Central Kuroshio, Solomon Islands, New Caledonia, and Vanuatu MEOWs. That is, the geographic distribution of the species extends much farther westward (Red Sea), northward (Japan) and southward (New Caledonia) than we were aware at the time of listing. Furthermore, as noted by Fujii et al. (2020), *F. paradivisa*'s distribution remains poorly documented because of the lack of surveys of low light habitats, including shallow turbid areas and mesophotic depths, and thus its geographic distribution is likely still underestimated.

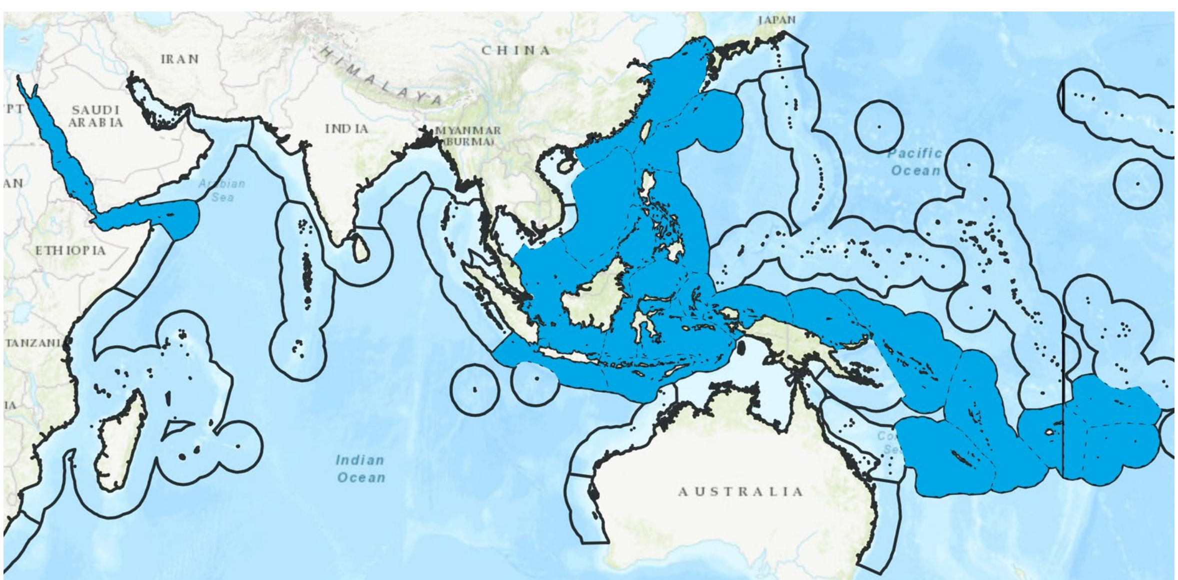


Figure 24. Geographic distribution of *F. paradivisa*.

Depth Distribution. Its confirmed depth distribution is 5–75 m (Turak et al. 2008, Muir and Pichon 2019). It has also been recorded from 6 m in Timor-Leste (Turak and DeVantier 2012), 25 m in American Samoa (NMFS 2020b), 30 m in Malaysia (Waheed and Hoeksema 2014), 49 m in American Samoa (Toonen and Montgomery 2018), 45–53 m in the northern Red Sea (Eyal et al. 2016), and 55 m in Japan (Sinnigar and Harii 2018). Thus, current information indicates that *F. paradivisa* has a much broader depth range (5–75 m) than we were aware of at the time of listing in 2014 (5–20 m).

U.S. Distribution. Within U.S. waters, *F. paradivisa* occurs on Tutuila in American Samoa (NMFS 2022b). American Samoa is within the Samoa MEOW (Spalding et al. 2007).

Relevance of Distribution to Status. Geographic and depth distributions were the key spatial factors considered in determining the status of coral species and in the listing of *F. paradivisa* in 2014. A narrow geographic or depth distribution exacerbates a species' extinction risk because larger proportions of the population are likely to be exposed to any single disturbance. In contrast, a broad overall distribution moderates a species' extinction risk because the population is distributed across a range of geographic areas and depths, and thus lower proportions of the populations are likely to be exposed to any single disturbance. For example, one reason that *F. paradivisa* was listed was because the information available at that time indicated a limited geographic distribution mainly in the Coral Triangle (79 FR 53851). Since both the geographic and depth distributions of *F. paradivisa* are greater than we were aware of at the time of listing in 2014, its distribution has a greater capacity to moderate extinction risk.

4.10.3. Abundance

Relative Abundance: DeVantier and Turak (2017) characterized abundances of over 600 Indo-Pacific reef-building coral species in 31 Veron ecoregions from the Red Sea to Fiji, as further described in Section 4.1.3 above. *Fimbriaphyllia paradivisa* was recorded in 4 of the 31 ecoregions. Within those 4 ecoregions, it had a mean overall abundance of 2.24 (Uncommon), ranging from 1.08 (Uncommon) in the Socotra Archipelago to 3.75 (Uncommon) in the Celebes Sea Ecoregion. The mean overall abundance of *F. paradivisa* for all 31 ecoregions was 0.42 (Rare, DeVantier and Turak 2017, Table S2), however some of the 27 ecoregions where it was not recorded may be outside its range. In addition, *F. paradivisa* is a near ubiquitous reef coral species in the upper mesophotic zone in the northern Red Sea (Eyal et al. 2016, Tamir et al. 2019), but it was not recorded at any of DeVantier and Turak's (2017) Red Sea sites, presumably because their surveys were too shallow (usually <40 m). In contrast to the Red Sea, upper mesophotic surveys in the Coral Triangle and adjacent areas only recorded *F. paradivisa* at one of 287 sites (Turak and DeVantier 2019). Within its range, the relative abundance of *F. paradivisa* may vary locally from very rare to near ubiquitous. However, based on the above information, the rangewide relative abundance of *F. paradivisa* is uncommon. Thus, current information indicates that *F. paradivisa* has a higher relative abundance (uncommon) than we were aware of at the time of listing in 2014 (rare).

Absolute Abundance. Absolute abundance is an estimate of the total number of colonies of a species that currently exist throughout its range. Based on *F. paradivisa'*s distribution and relative abundance, NMFS (2014) estimated the absolute abundance of *F. paradivisa* to be at least tens of millions of colonies. However, that estimate was based on assumptions that *F. paradivisa*'s distribution was much smaller, and its abundance lower, than shown by the recent information cited above. Based on the methodology used in NMFS (2014) and the current distribution and abundance information, *F. paradivisa*'s absolute abundance is estimated to be at least hundreds of millions of colonies. Thus, current information indicates that *F. paradivisa* has a higher absolute abundance (at least hundreds of millions) than we were aware of at the time of listing in 2014 (at least tens of millions).

Abundance Trends. As described above in the general Threats Evaluation and below for threats to *F. paradivisa*, most threats have worsened since 2014. However, no genus or species-specific data are available for abundance trends of *Fimbriaphyllia* or *F. paradivisa* before or since 2014, including responses to the worsening threats.

Relevance of Abundance to Status. Abundance is the key demographic factor considered in determining the status of coral species and in the listing of *F. paradivisa* in 2014. A low relative or absolute abundance, especially in combination with declining abundance, exacerbates a species' extinction risk because larger proportions of the population are likely to be exposed to any single disturbance. In contrast, a higher relative or absolute abundance moderates a species' extinction risk because lower proportions of the population are likely to be exposed to any single disturbance (79 FR 53851). Since the relative and absolute abundances of *F. paradivisa* are both greater than we were aware of in at the time of listing in 2014, its abundance may have a greater capacity to moderate extinction risk.

4.10.4. Threats

This section provides an updated threats evaluation for *F. paradivisa*, focusing on the threats that contributed to its listing (79 FR 53851), which included ocean warming, ocean acidification, disease, fishing, LBSP, predation, collection and trade, and inadequacy of existing regulatory mechanisms. A threats summary table is provided, including relative importance ratings for the threats, effects of threats since listing in 2014, and projected effects of threats in the foreseeable future.

Ocean Warming: As noted in Section 3.2.1 above, since listing in 2014, the effects of ocean warming on Indo-Pacific reef-building corals in general have substantially worsened. *Fimbriaphyllia* corals have been heavily bleached by past warming events (79 FR 53851), and Pratchett et al. (2020) found that *F. glabrescens* had moderate bleaching susceptibility to elevated seawater temperature. In a laboratory study of *F. paradivisa* collected from the mesophotic zone in the Red Sea, colonies survived for extended periods of time with no zooxanthellae, providing evidence of the species' potential to survive disturbances such as warming-induced bleaching (Eyal et al. 2016). However, whether that means *F. paradivisa* has lower susceptibility to ocean warming is unknown. Section 3.2.1 also describes how ocean warming is projected to greatly worsen in the foreseeable future (i.e., between now and 2100).

In conclusion, while the current information indicates potentially lower susceptibility of *F. paradivisa* to ocean warming, the information is sparse and inconclusive. Thus, we still conclude that the species is susceptible to this threat. Furthermore, ocean warming has substantially worsened since listing in 2014, and it is likely to greatly worsen in the foreseeable future (Table 13).

Ocean Acidification: As noted in Section 3.2.2 above, since listing in 2014, the effects of ocean acidification on Indo-Pacific reef-building corals have worsened. Generally, *Fimbriaphyllia* corals are thought to have some susceptibility to ocean acidification (79 FR 53851). While new information since the 2014 listing indicates that some *Fimbriaphyllia* corals occur in naturally low pH environments (Barkley et al. 2015, van Woesik and Cacciapaglia 2018, Maggioni et al. 2021), whether that means *F. paradivisa* generally has low susceptibility to ocean acidification is unknown. Section 3.2.2 also describes how ocean acidification is projected to greatly worsen in the foreseeable future. In conclusion, while the current information indicates potentially lower susceptibility of *F. paradivisa* to ocean acidification, there is no species-specific information. Thus, we still conclude that the species is susceptible to this threat. Furthermore, ocean acidification has worsened since listing in 2014, and it is likely to greatly worsen in the foreseeable future (Table 13).

Disease: As noted in Section 3.2.3 above, since listing in 2014, the effects of disease on Indo-Pacific corals have increased, mainly in response to the 2014 – 2017 bleaching events. Generally, *Fimbriaphyllia* corals were thought to have some susceptibility to disease (79 FR 53851). Section 3.2.3 also describes how disease is projected to substantially worsen in the foreseeable future. In conclusion, the current information indicates that *F. paradivisa* continues to be susceptible to disease, that this threat has worsened since listing in 2014, and that it will substantially worsen in the foreseeable future (Table 13).

Fishing: As noted in Section 3.2.4 above, since listing in 2014, the direct and indirect effects of fishing on Indo-Pacific corals have continued, likely intensifying in some locations while lessening in others due to various factors. Branching corals such as most *Fimbriaphyllia* species may be more susceptible than other corals to damage by fishing gear because of their morphology (Brainard et al. 2011, 79 FR 53851). Section 3.2.4 also describes how fishing is projected to substantially worsen in the foreseeable future. In conclusion, the current information indicates that *F. paradivisa* continues to be susceptible to fishing, that this threat has continued since listing in 2014, and that it will substantially worsen in the foreseeable future (Table 4).

LBSP: As noted in Section 3.2.5 above, since listing in 2014, the effects of LBSP on Indo-Pacific corals have continued, likely intensifying in some locations while lessening in others due to various factors. Generally, *Fimbriaphyllia* corals were thought to have some susceptibility to LBSP (79 FR 53851). However, as noted above in the Biology section, new information since the 2014 listing indicates that *F. paradivisa* commonly occurs in turbid, high-sediment environments (Fenner 2020a, Fujii et al. 2020, Sinniger and Harii 2018). Therefore, the current information indicates that *F. paradivisa* is less susceptible to the effects of LBSP than we were aware of at the time of listing in 2014. Section 3.2.5 also describes how LBSP is projected to substantially worsen in the foreseeable future. In conclusion, while the current information indicates lower susceptibility of *F. paradivisa* to LBSP than we were aware of at the time of listing in 2014. Thus we conclude that LBSP has lower relative importance to the extinction risk of *F. paradivisa* (i.e., Low instead of Low-Medium) than for the other 14 listed species. However, LBSP is likely to substantially worsen in the foreseeable future (Table 13).

Predation: As noted in Section 3.2.6 above, since listing in 2014, the effects of predation on Indo-Pacific corals have increased, mainly because the 2014 – 2017 bleaching events resulted in more favorable conditions for predators such as COTS. Generally, *Fimbriaphyllia* corals were thought to have some susceptibility to predation (79 FR 53851). Section 3.2.6 also describes how predation is projected to substantially worsen in the foreseeable future. In conclusion, the current information indicates that *F. paradivisa* continues to be susceptible to predation, that this threat has worsened since listing in 2014, and that it will substantially worsen in the foreseeable future (Table 13).

Collection and Trade: As noted in Section 3.2.7 above, since listing in 2014, the effects of collection and trade on Indo-Pacific corals have continued. Corals knowns as *Euphyllia* are some of the most popular in the marine aquarium industry, including what is known in the industry as "*Euphyllia paradivisa*" (i.e., *F. paradivisa*, Blake 2022). According to the CITES database cited in Section 3.2.7, since 1990 hundreds of thousands of *Euphyllia* units were globally imported and exported annually. These units were not identified to species, thus likely included an undeterminable number of unidentified *F. paradivisa*. In addition, the database also records that between about 3,000 and 21,000 "*Euphyllia paradivisa*" (i.e., *F. paradivisa*) units were globally imported and exported annually from 1990 to 2017 (NMFS 2022a). Because of the popularity of *Euphyllia* corals in the marine aquarium trade (Blake 2022) as well as the ongoing and projected growth in the industry, collection and trade may increasingly impact the status of *F. paradivisa*. Section 3.2.7 also describes how collection and trade is projected to substantially worsen in the foreseeable future. In conclusion, the current information indicates that *F. paradivisa* continues to be susceptible to collection and trade, that this threat has continued since listing in 2014, and that it will substantially worsen in the foreseeable future (Table 13).

Sea-level Rise: As noted in Section 3.2.8 above, since listing in 2014, sea-level rise has likely been too gradual to result in measurable effects on Indo-Pacific reef-building corals. In those cases where earthquakes have resulted in substrate uplift resembling sea-level rise, these substrates have been colonized by rapidly-growing corals. In conclusion, as in the final rule, the current information indicates that *F. paradivisa* is not susceptible to sea-level rise, that there have been no detectable trends in the effects of this threat since listing in 2014, but that it will worsen in the foreseeable future (Table 13).

Regulatory Mechanisms: As noted in Section 3.2.9 above, since listing in 2014, some progress has been made with GHG management as well as controlling local threats although existing regulatory mechanisms are still inadequate to control any of the threats. Section 3.2.9 also describes how it is unlikely that regulatory mechanisms will be improved to the point where they are adequate to control any of the threats in the foreseeable future. In conclusion, the current information indicates that existing regulatory mechanisms remain inadequate to control any threat to *F. paradivisa*, and that improvement is unlikely in the foreseeable future (Table 13).

Threats Conclusion for *F. paradivisa*: Since *F. paradivisa* was listed in 2014, many of the threats to the species have worsened. All threats are projected to worsen in the foreseeable future, with the possible exception of regulatory mechanisms, which may continue to improve but also are likely to remain inadequate for controlling any of the threats (Table 13).

Although the final rule rated the relative importance of threats to the world's reef-building corals (Table 2), it did not apply those ratings to *F. paradivisa* (79 FR 53851). Instead, the final rule concluded that *F. paradivisa* is susceptible to ocean warming, ocean acidification, disease, fishing, LBSP, predation, and collection and trade, while regulatory mechanisms were inadequate for controlling any threat (79 FR 53851). However, as summarized above, we now have more genus-specific and species-specific information available on the importance of each threat to *Fimbriaphyllia* species and *F. paradivisa*, respectively. Based on the general importance ratings of the threats to Indo-Pacific reef-building corals (Table 3) and the genus-specific and species-specific information above, we conclude that the relative importance ratings of each threat to Indo-Pacific corals apply to *F. paradivisa* with the exception of LBSP (rated as Low instead of Low-Medium, as explained in the LBSP paragraph above). In addition, the observed threat trends since 2014 and projected threat trends in the foreseeable future are provided (Table 13).

Table 13. Summary of threats evaluation for *F. paradivisa*. For each threat, relative importance to the extinction risk of the species, observed trend since 2014, and projected trend in the foreseeable future are provided.

Threat (listing factor)	Importance	Observed Trend in Effects Since 2014	Projected Trend in Effects to 2100
Ocean Warming (Factor E)	Very High	Substantially worsened	Greatly worsen
Ocean Acidification (Factor E)	High	Worsened	Greatly worsen
Disease (Factor C)	High	Worsened	Substantially worsen
Fishing (Factor A)	Medium	Continued	Substantially worsen
LBSP (Factors A and E)	Low	Continued	Substantially worsen
Predation (Factor C)	Low-Medium	Worsened	Substantially worsen
Collection and Trade (Factor B)	Low-Medium	Continued	Substantially worsen
Sea-level Rise (Factor E)	Low	No detectable trends	Worsen
Inadequacy of Existing Regulatory Mechanisms (Factor D)	High	Some improvement but still inadequate	Improvement but likely still inadequate

4.10.5. Conclusion

As explained in the 2014 final listing rule (79 FR 53851), a species' vulnerability to extinction results from the combination of its spatial (i.e., distribution) and demographic (i.e., abundance) characteristics, threat susceptibilities, and consideration of the baseline environment and future projections of threats. *Fimbriaphyllia paradivisa* was listed as threatened in 2014 (as *Euphyllia paradivisa*) because of its limited geographic distribution largely restricted to the Coral Triangle, low abundance, susceptibilities to ocean warming, ocean acidification, fishing, LBSP, disease, predation, and collection and trade, inadequate regulatory mechanisms, declining baseline conditions, and projected worsening of threats (79 FR 53851).

Since 2014, we have learned that *F. paradivisa* has: (1) a much broader geographic distribution (24 MEOWs instead of 15); (2) a much broader depth range (5–75 m instead of 5–20 m); (3) higher overall relative abundance (uncommon instead of rare); and (4) higher absolute abundance (at least hundreds of millions of colonies instead of at least tens of millions) than we believed in 2014. That is, *F. paradivisa* is more broadly distributed and more abundant than we believed in 2014, and thus may have a higher capacity to moderate the effects of the threats, as explained in the Relevance of Distribution/Abundance to Status sections above.

Since 2014, the effects of most threats have worsened. All threats are projected to substantially worsen under current global GHG regulatory mechanisms, which would result in global warming of 2.6–3.4°C above the pre-industrial baseline by 2100 (see Fig. 4 in Section 3.1 above). Even if the goal of the Paris Agreement is achieved (i.e., limiting global warming to 1.5°C above pre-industrial by 2100), the threats would become much worse than they are currently (Dixon et al. 2022), potentially preventing the recovery of *F. paradivisa*. Current regulatory mechanisms are grossly inadequate, especially GHG management.

In conclusion, the above information shows that *F. paradivisa* is much more broadly distributed and more abundant than we believed in 2014, but that the threats have worsened. Especially concerning is that the most important threat to the species, ocean warming, has substantially worsened since the species was listed in 2014. The other important threats to the species, including ocean acidification, disease, fishing, predation, and collection and trade have also either worsened or continued since 2014. While there has been some progress with regulatory mechanisms, primarily because of the 2016 Paris Agreement, regulatory mechanisms for both global and local threats are still inadequate. However, the species' distribution is much broader and its abundance is greater than we were aware of at the time of listing in 2014, both of which are key factors for moderating threats.

4.11. *Isopora crateriformis* (Gardiner 1898)

4.11.1. Biology

Taxonomy. This species was originally described as *Madrepora crateriformis* (Gardiner 1898). Studer (1879) named *Isopora* as a subgenus to *Madrepora*, but did not include *M. crateriformis* in *Isopora*. Verrill (1902) assigned all *Madrepora* species including *M. crateriformis* to the genus *Acropora* (Verrill 1902). It was included as *Acropora (Isopora) crateriformis* in Wallace and Wolstenholme (1998) and Wallace (1999), and as *A. crateriformis* in Veron (2000). *Isopora* remained a subgenus of *Acropora* until Wallace et al. (2007) presented clear evidence that *Isopora* is a separate, valid genus. Since that time, *Isopora* has been treated as a genus, including *I. crateriformis* (Wallace et al. 2012, Veron et al. 2016), which is accepted by WoRMS (Hoeksma and Cairns 2021).

Morphology. *Isopora crateriformis* forms flattened, solid, encrusting plates, usually with ripples on the surface. Most colonies are tan, but a few have tiny green spots, which are the retracted polyps (Fig. 25). Colonies are usually up to about 40 cm diameter but can be over 1 m diameter. Corallites are 1-2 mm in diameter, rounded projecting tubes, larger on the ridges and smaller between. When a colony occurs on a slope, the lower edge is often lifted as a plate (Fenner and Burdick 2016, Veron 2000). This species is similar to some other *Isopora* species, but *I. crateriformis* has distinctive characteristics that can usually be reliably identified in the field. However, it is not distinguishable from juvenile, unbranched *I. cuneata*, as described in Fenner and Burdick (2016).

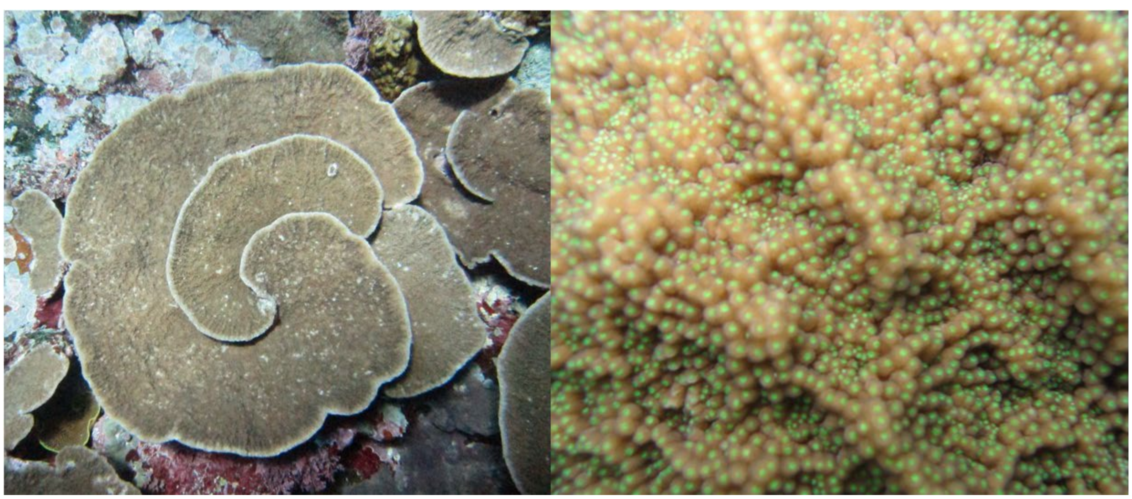


Figure 25. *Isopora crateriformis*, showing colony morphology. Photos are from Tutuila, American Samoa (photos copyright, Doug Fenner).

Habitat. *Isopora crateriformis* is typically found on shallow forereefs, but may also occur in backreef areas with strong wave action such as the outer margins of reef flats (NMFS 2022b). The Coral Traits Database (https://coraltraits.org/, accessed August 2022) lists *I. crateriformis*'s water clarity preference as "clear," and wave exposure preference as "exposed."

Life History. The life history of *I. crateriformis* has not been studied; however, it is most likely a hermaphroditic brooder based on studies of other *Isopora* species. Brooders release sperm but fertilization and larval development are internal. In contrast, *Acropora* species are broadcast spawners, one of the key differences that led to elevation of *Isopora* from an *Acropora* subgenus to genus (Wallace et al. 2007). *Isopora* species' brooding life histories allow them to locally dominate coral communities at Lord Howe Island, Australia (Harriott 1992). The same may be true of *I. crateriformis* on Tutuila, American Samoa, where the species is locally dominant on some upper reef slopes (Fenner 2020a,b). A study of skeletal growth in *I. palifera* on the central GBR showed annual linear extension rates of approximately 2.1 cm (Razak et al. 2017).

4.11.2. Distribution

Geographic Distribution. *Isopora crateriformis* has a relatively limited geographic distribution, occurring in 27 MEOWs (Fig. 26), based on information in NMFS (2022c). The majority of its distribution is restricted to the Coral Triangle and western equatorial Pacific, which is projected to have the most rapid and severe impacts from climate change and localized human impacts for coral reefs over the 21st century. The distribution of the species within U.S. waters is summarized below. The current information indicates that *I. crateriformis* occurs in one more MEOW (Bonaparte Coast of northern Australia) and thus has a slightly larger geographic distribution than we were aware of at the time of listing in 2014 (NMFS 2022c).

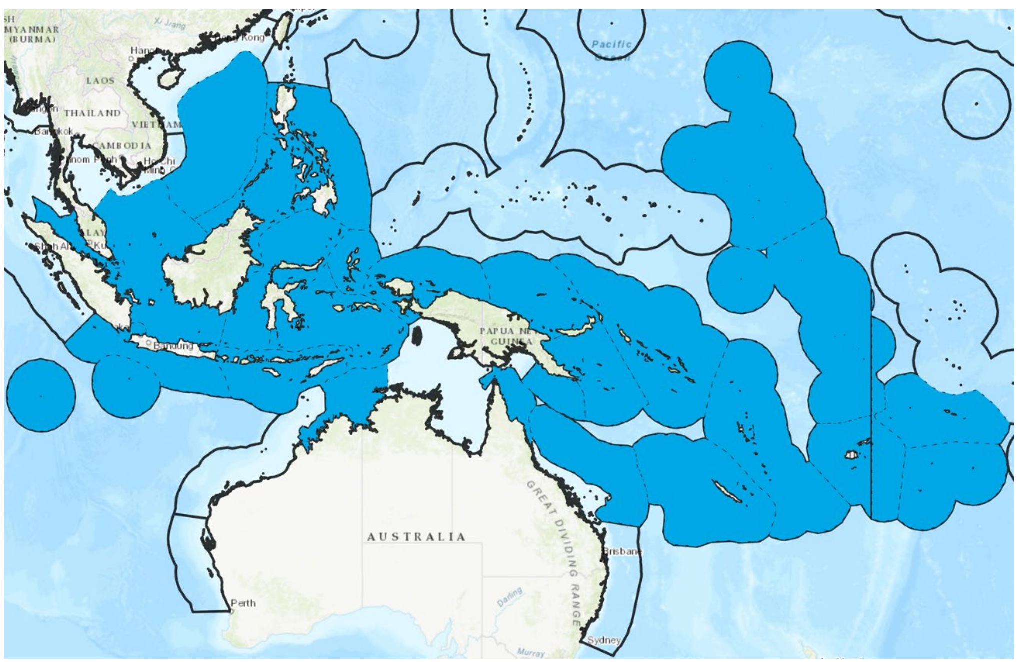


Figure 26. Geographic distribution of *I. crateriformis*.

Depth Distribution. On Tutuila, American Samoa, the species is most common at 0–12 m of depth (Fenner 2020a), but has been recorded to 20 m (NMFS 2022b). The Coral Traits Database (https://coraltraits.org/, accessed August 2022) lists *I. crateriformis*'s maximum recorded depth as 25 m. Thus, current information indicates that *I. crateriformis* has approximately twice as large a depth range (0–25 m) than we were aware of at the time of listing in 2014 (0–12 m).

U.S. Distribution. *Isopora crateriformis* occurs on Tutuila, Ofu, Olosega and Ta'u in American Samoa but has not been recorded elsewhere within U.S. waters (NMFS 2022b). American Samoa is within the Samoa MEOW (Spalding et al. 2007).

Relevance of Distribution to Status. Geographic and depth distributions were the key spatial factors considered in determining the status of coral species and in the listing of *I. crateriformis* in 2014. A narrow geographic or depth distribution exacerbates a species' extinction risk because larger proportions of the population are likely to be exposed to any single disturbance. In contrast, a broad overall distribution moderates a species' extinction risk because the population is distributed across a range of geographic areas and depths, and thus lower proportions of the populations are likely to be exposed to any single disturbance. For example, one reason that *I. crateriformis* was listed was because the information available at that time indicated a narrow depth distribution of 0–12 m (79 FR 53851). Since both the geographic and depth distributions of *I. crateriformis* are greater than we were aware of at the time of listing in 2014, its distribution has a greater capacity to moderate extinction risk.

4.11.3. Abundance

Relative Abundance: DeVantier and Turak (2017) characterized abundances of over 600 Indo-Pacific reef-building coral species in 31 Veron ecoregions from the Red Sea to Fiji, as further described in Section 4.1.3 above. *Isopora crateriformis* was recorded in 5 of the 31 ecoregions. Within those 5 ecoregions, it had a mean overall abundance of 2.98 (Uncommon), ranging from 1.34 (Uncommon) in the Sulu Sea Ecoregion to 6.52 (Uncommon) in the Fiji Ecoregion. The mean overall abundance of *I. crateriformis* for all 31 ecoregions was 0.46 (Rare, DeVantier and Turak 2017, Table S2), however some of the 26 ecoregions where it was not recorded may be outside its range. The Coral Traits Database (https://coraltraits.org/, accessed August 2022) lists *I. crateriformis*'s global relative abundance as "common," but does not cite DeVantier and Turak (2017). Wallace (1999) and the Corals of the World website (http://www.coralsoftheworld.org/, accessed August 2022) note that *I. crateriformis* is common in parts of Indonesia, while Harriott (1992) and Fenner (2020a,b) note that the species is locally dominant on Lord Howe Island, Australia, and Tutuila, American Samoa, respectively. Within its range, the relative abundance of *I. crateriformis* may vary locally from very rare to near ubiquitous. However, based on the above information, the rangewide relative abundance of *I. crateriformis* is uncommon to common. Thus, current information indicates that *I. crateriformis* has a higher relative abundance (uncommon to common) than we were aware of at the time of listing in 2014 (rare).

Absolute Abundance. Absolute abundance is an estimate of the total number of colonies of a species that currently exist throughout its range. Based on *I. crateriformis'*s distribution and relative abundance, NMFS (2014) estimated the absolute abundance of *I. crateriformis* to be at least millions of colonies. Dietzel et al. (2021) estimated its absolute abundance at 69.6 million colonies. Muir et al. (2022) argued that the data were unsuitable to provide such quantitative estimates, and Dietzel et al.'s (2022) reply agreed that better data are needed. Based on the updated information, *I. crateriformis'*s absolute abundance is likely to be at least tens of millions of colonies. Thus, current information indicates that *I. crateriformis* has a higher absolute abundance (at least tens of millions) than we were aware of at the time of listing in 2014 (at least millions).

Abundance Trends. When *I. crateriformis* was listed in 2014, it was thought to have a decreasing abundance trend across its range over at least the past several decades, based on overall declines in coral cover and the susceptibility of *I. crateriformis* to the worst threats. At that time, we were not aware of any time-series abundance trend data for this species (79 FR 53851). Since then, we learned of coral species survey results from Fagatele Bay in the National Marine Sanctuary of American Samoa on the southern tip of Tutuila, where surveys of the same 6 fixed transects from 3–

12 m depth were periodically conducted. The total numbers of *I. crateriformis* colonies were 44 in 1995, 13 in 2002, and 50 in 2018 (Chuck Birkeland, personal communication, April 2021). The monitoring program is designed to monitor coral trends on the spatial scale of Fagatele Bay (i.e., reef scale), and may or may not reflect abundance trends on larger spatial scales, such as island, archipelago or MEOW scales.

As described above in the general Threats Evaluation and below for threats to *I. crateriformis*, the most important threats (i.e., ocean warming, ocean acidification) have worsened since 2014, and substantial impacts to *Isopora* species including *I. crateriformis* have been documented. Based on the continued worsening in the most important threats, it is likely that *I. crateriformis* is decreasing in overall abundance (i.e., abundance across all the ecoregions that make up its range).

Relevance of Abundance to Status. Abundance is the key demographic factor considered in determining the status of coral species and in the listing of *I. crateriformis* in 2014. A low relative or absolute abundance, especially in combination with declining abundance, exacerbates a species' extinction risk because larger proportions of the population are likely to be exposed to any single disturbance. In contrast, a higher relative or absolute abundance moderates a species' extinction risk because lower proportions of the population are likely to be exposed to any single disturbance (79 FR 53851). Since both the relative abundance and absolute abundance of *I. crateriformis* are greater than we were aware of in at the time of listing in 2014, its abundance may have a greater capacity to moderate extinction risk.

4.11.4. Threats

This section provides an updated threats evaluation for *I. crateriformis*, focusing on the threats that contributed to its listing (79 FR 53851), including ocean warming, ocean acidification, disease, fishing, LBSP, predation, and inadequacy of existing regulatory mechanisms. In addition, current information indicates that collection and trade is also impacting the status of the species. A threats summary table is provided, including relative importance ratings for the threats, effects of threats since listing in 2014, and projected effects of threats in the foreseeable future.

Ocean Warming: As noted in Section 3.2.1 above, since listing in 2014, the effects of ocean warming on Indo-Pacific reef-building corals in general have substantially worsened. In response to the 2014–2017 series of warming-induced bleaching events, *Isopora* corals were generally among the most impacted coral taxa in different locations around the Indo-Pacific (e.g., Frade et al 2018, Hughes et al 2018a, Gilmour et al. 2022). In a study of the changes in the GBR's coral communities, which is within *I. crateriformis*'s range, between 1995/96 and 2016/17, Dietzel et al. (2020) found that *Isopora* species declined by 38.5% on the reef crest and 52.5% on the reef slope (6–7 m depth). A study of the changes in response to multiple warming-induced coral bleachings in the Chagos Islands between 1979 and 1998 found that while total coral cover was reduced by approximately 50%, cover of *I. palifera* was reduced by approximately 90% (Sheppard et al. 2020). Section 3.2.1 also describes how ocean warming is projected to greatly worsen in the foreseeable future (i.e., between now and 2100).

With regard to impacts of this threat on *I. crateriformis*, a model based on species' responses to the 2016 bleaching event found that *I. crateriformis* is at high extinction risk from warming-induced bleaching because of its shallow depth distribution (Muir et al. 2017). In conclusion, the current information indicates that *I. crateriformis* continues to be highly susceptible to ocean warming, that this threat has substantially worsened since listing in 2014, and that it will greatly worsen in the foreseeable future (Table 14).

Ocean Acidification: As noted in Section 3.2.2 above, since listing in 2014, the effects of ocean acidification on Indo-Pacific reef-building corals have worsened. Generally, *Isopora* corals are thought to have some susceptibility to ocean acidification (79 FR 53851), and laboratory experiments have found that *I. palifera* bleaches in response to ocean acidification levels that are projected in the foreseeable future (Iguchi et al. 2014, Yang et al. 2020). Section 3.2.2 also describes how ocean acidification is projected to greatly worsen in the foreseeable future. In conclusion, the current information indicates that *I. crateriformis* continues to be susceptible to ocean acidification, that this threat has worsened since listing in 2014, and that it will greatly worsen in the foreseeable future (Table 14).

Disease: As noted in Section 3.2.3 above, since listing in 2014, the effects of disease on Indo-Pacific corals have increased, mainly in response to the 2014–2017 bleaching events. Generally, *Isopora* corals are thought to have some susceptibility to disease (79 FR 53851). Section 3.2.3 also describes how disease is projected to substantially worsen in the foreseeable future. In conclusion, the current information indicates that *I. crateriformis* continues to be susceptible to disease, that this threat has worsened since listing in 2014, and that it will substantially worsen in the foreseeable future (Table 14).

Fishing: As noted in Section 3.2.4 above, since listing in 2014, the direct and indirect effects of fishing on Indo-Pacific corals have continued, likely intensifying in some locations while lessening in others due to various factors. Generally, *Isopora* corals are thought to have some susceptibility to fishing (79 FR 53851). Section 3.2.4 also describes how fishing is projected to substantially worsen in the foreseeable future. In conclusion, the current information indicates that *I. crateriformis* continues to be susceptible to fishing, that this threat has continued since listing in 2014, and that it will substantially worsen in the foreseeable future (Table 14).

LBSP: As noted in Section 3.2.5 above, since listing in 2014, the effects of LBSP on Indo-Pacific corals have continued, likely intensifying in some locations while lessening in others due to various factors. Generally, *Isopora* species are relatively susceptible to sediment and nutrients, compared to other reef-building coral taxa (Brainard et al. 2011, 79 FR 53851). Section 3.2.5 also describes how LBSP is projected to substantially worsen in the foreseeable future. In conclusion, the current information indicates that *I. crateriformis* continues to be susceptible to LBSP, that this threat has continued since listing in 2014, and that it will substantially worsen in the foreseeable future (Table 14).

Predation: As noted in Section 3.2.6 above, since listing in 2014, the effects of predation on Indo-Pacific corals have increased, mainly because the 2014–2017 bleaching events resulted in more favorable conditions for predators such as COTS. Generally, *Isopora* corals are thought to have some susceptibility to predation (79 FR 53851). Section 3.2.6 also describes how predation is projected to substantially worsen in the foreseeable future. In conclusion, the current information indicates that *I. crateriformis* continues to be susceptible to predation, that this threat has worsened since listing in 2014, and that it will substantially worsen in the foreseeable future (Table 14).

Collection and Trade: Although collection and trade did not contribute to the listing of *I. crateriformis* (79 FR 53851), the following information indicates that this threat is likely impacting the status of the species. As noted in Section 3.2.7 above, since listing in 2014, the effects of collection and trade on Indo-Pacific corals have continued. According to the CITES database cited in Section 3.2.7, between 1989 and 2017, between a few hundred and over 10,000 *Isopora* units were globally imported and exported annually. These units were not identified to species, thus may have included an undeterminable number of unidentified *I. crateriformis*. In addition, the database also records that in 2010 and 2011, a few dozen *I. crateriformis* units were globally imported and exported annually (NMFS 2022a). Because of the ongoing and projected growth in the industry, collection and trade may increasingly impact the status of *I. crateriformis*. Section 3.2.7 also describes how collection and trade is projected to substantially worsen in the foreseeable future. In conclusion, the current information indicates that *I. crateriformis* is susceptible to collection and trade, that this threat has continued since listing in 2014, and that it will substantially worsen in the foreseeable future (Table 14).

Sea-level Rise: As noted in Section 3.2.8 above, since listing in 2014, sea-level rise has likely been too gradual to result in measurable effects on Indo-Pacific reef-building corals. In those cases where earthquakes have resulted in substrate uplift resembling sea-level rise, these substrates have been colonized by rapidly-growing corals like *Isopora* species. In conclusion, as in the final rule, the current information indicates that *I. crateriformis* is not susceptible to sea-level rise, that there have been no detectable trends in the effects of this threat since listing in 2014, but that it will worsen in the foreseeable future (Table 14).

Regulatory Mechanisms: As noted in Section 3.2.9 above, since listing in 2014, some progress has been made with GHG management as well as controlling local threats although existing regulatory mechanisms are still inadequate to control any of the threats. Section 3.2.9 also describes how it is unlikely that regulatory mechanisms will be improved to the point where they are adequate to control any of the threats in the foreseeable future. In conclusion, the current information indicates that existing regulatory mechanisms remain inadequate to control any threat to *I. crateriformis*, and that improvement is unlikely in the foreseeable future (Table 14).

Threats Conclusion for *I. crateriformis*: Since *I. crateriformis* was listed in 2014, many of the threats to the species have worsened. All threats are projected to worsen in the foreseeable future, with the possible exception of regulatory mechanisms, which may continue to improve but also are likely to remain inadequate for controlling any of the threats (Table 14).

Although the final rule rated the relative importance of threats to the world's reef-building corals (Table 2), it did not apply those ratings to *I. crateriformis* (79 FR 53851). Instead, the final rule concluded that *I. crateriformis* is highly susceptible to ocean warming, and susceptible to ocean acidification, disease, fishing, LBSP, and predation, while regulatory mechanisms were inadequate for controlling any threat (79 FR 53851). However, as summarized above, we now have more genus-specific and species-specific information available on the importance of each threat to *Isopora* species and *I. crateriformis*, respectively. Based on the general importance ratings of the threats to Indo-Pacific reef-building corals (Table 3) and the genus-specific and species-specific information above, we conclude that the relative importance ratings of each threat to Indo-Pacific corals apply to *I. crateriformis*. In addition, the observed threat trends since 2014 and projected threat trends in the foreseeable future are provided (Table 14).

Table 14. Summary of threats evaluation for *I. crateriformis*. For each threat, relative importance to the extinction risk of the species, observed trend since 2014, and projected trend in the foreseeable future are provided.

Threat (listing factor)	Importance	Observed Trend in Effects Since 2014	Projected Trend in Effects to 2100
Ocean Warming (Factor E)	Very High	Substantially worsened	Greatly worsen
Ocean Acidification (Factor E)	High	Worsened	Greatly worsen
Disease (Factor C)	High	Worsened	Substantially worsen
Fishing (Factor A)	Medium	Continued	Substantially worsen
LBSP (Factors A and E)	Low-Medium	Continued	Substantially worsen
Predation (Factor C)	Low-Medium	Worsened	Substantially worsen
Collection and Trade (Factor B)	Low-Medium	Continued	Substantially worsen
Sea-level Rise (Factor E)	Low	No detectable trends	Worsen
Inadequacy of Existing Regulatory Mechanisms (Factor D)	High	Some improvement but still inadequate	Improvement but likely still inadequate

4.11.5. Conclusion

As explained in the 2014 final listing rule (79 FR 53851), a species' vulnerability to extinction results from the combination of its spatial (i.e., distribution) and demographic (i.e., abundance) characteristics, threat susceptibilities, and consideration of the baseline environment and future projections of threats. *Isopora crateriformis* was listed as threatened in 2014 because of its limited geographic distribution largely restricted to the Coral Triangle and western equatorial Pacific, low abundance, high susceptibility to ocean warming, susceptibilities to ocean acidification, fishing, LBSP, disease, and predation, inadequate regulatory mechanisms, declining baseline conditions, and projected worsening of threats (79 FR 53851).

Since 2014, we have learned that *I. crateriformis* has: (1) a broader geographic distribution (27 MEOWs instead of 26); (2) a broader depth range (0–25 m instead of 0–12 m); (3) higher relative abundance (uncommon to common instead of rare); and (4) higher absolute abundance (at least tens of millions of colonies instead of at least millions of colonies). That is, *I. crateriformis* is more broadly distributed and more abundant than we believed in 2014, and thus may have a higher capacity to moderate the effects of the threats, as explained in the Relevance of Distribution/Abundance to Status sections above.

Since 2014, the effects of ocean warming have substantially worsened, and the effects of most other threats have worsened as well. All threats are projected to substantially worsen under current global GHG regulatory mechanisms, which would result in global warming of 2.6–3.4°C above the pre-industrial baseline by 2100 (see Fig. 4 in Section 3.1 above). Even if the goal of the Paris Agreement is achieved (i.e., limiting global warming to 1.5°C above pre-industrial by 2100), the threats would become much worse than they are currently (Dixon et al. 2022), likely preventing the recovery of *I. crateriformis*. Current regulatory mechanisms are grossly inadequate, especially GHG management.

In conclusion, the above information shows that *I. crateriformis* is more broadly distributed and more abundant than we believed in 2014, but that the threats have worsened and that collection and trade is also an important threat to the species. Especially concerning is that the most important threat to the species, ocean warming, has substantially worsened since the species was listed in 2014. The other important threats to the species, including ocean acidification, disease, fishing, LBSP, predation, and collection and trade have also either worsened or continued since 2014. While there has been some progress with regulatory mechanisms, primarily because of the 2016 Paris Agreement, regulatory mechanisms for both global and local threats are still inadequate. However, the species' distribution is broader and its abundance is greater than we were aware of at the time of listing in 2014, both of which are key factors for moderating threats.

4.12. *Montipora australiensis* (Bernard 1897)

4.12.1. Biology

Taxonomy. *Montipora australiensis* was described by Bernard (1897), and is included in Veron and Wallace's (1984) review of Acroporidae (*Montipora, Anacropora, Acropora*, and *Astreopora* species) in eastern Australia. It is included in the Corals of the World books (Veron 2000) and website (http://www.coralsoftheworld.org/, accessed August 2022), and is accepted by WoRMS (Hoeksma and Cairns 2021).

Morphology. Colonies form thick plates and irregular columns, and are pale brown in color. The corallites are joined by a network of fine ridges (Fig. 27, Veron et al. 2016).

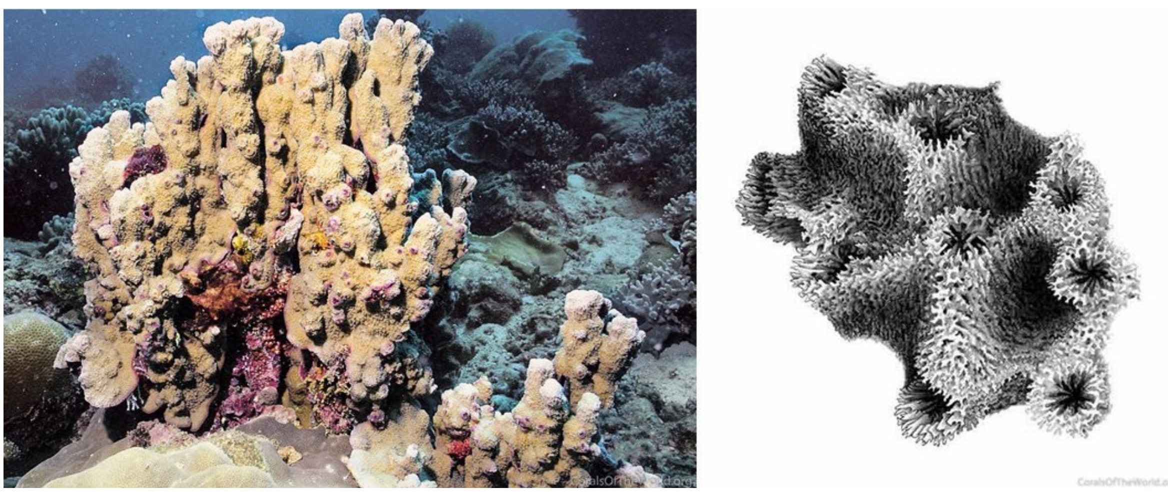


Figure 27. *Montipora australiensis*, showing colony and corallite morphology. Colony photo from the GBR (Charlie Veron), corallite drawing by Geoff Kelly (Veron et al. 2016).

Habitat. *Montipora australiensis* is found predominantly on upper reef slopes, lower reef crests, and reef flats, and it likely also occurs on mid-slopes and possibly other habitats (Brainard et al. 2011, 79 FR 53851). The Coral Traits Database (https://coraltraits.org/, accessed August 2022) lists *M. australiensis*'s water clarity preference as "clear," and wave exposure preference as "exposed."

Life History. Little information is available on the life history of *M. australiensis*. Like *Acropora* species, *Montipora* species are hermaphroditic broadcast spawners, whereby both male and female gametes into the water column and fertilization takes place externally. Larvae settle on suitable substrates such as rock or dead coral and grow into colonies (Brainard et al. 2011, 79 FR 53851).

4.12.2. Distribution

Geographic Distribution. *Montipora australiensis* has a relatively broad distribution (the second-most broadly distributed of the 15 species reviewed in this document after *A. globiceps*), occuring in 36 MEOWs (Fig. 28) but not in U.S. waters, based on information in NMFS (2022c). Its distribution is restricted largely to parts of the Coral Triangle and the western Indian Ocean. Despite the large number of islands and environments that are included in the species' range, it is mostly limited to an area projected to have the most rapid and severe impacts from climate change and localized human impacts for coral reefs over the 21st century.

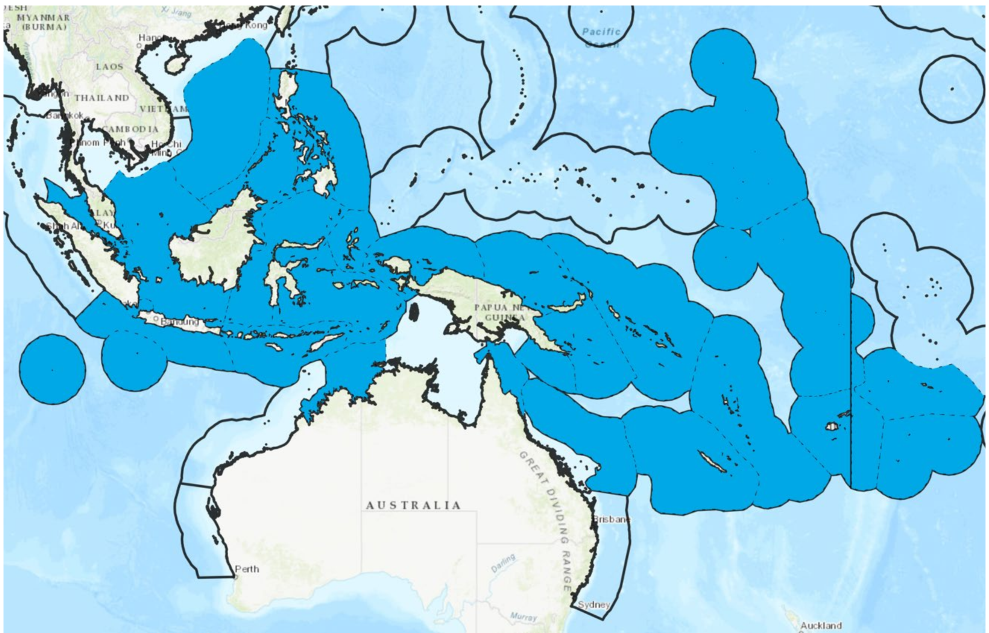


Figure 28. Geographic distribution of *M. australiensis*.

Depth Distribution. *Montipora australiensis* occurs at depths of approximately 2–30 m (79 FR 53851, Coral Traits Database https://coraltraits.org/, accessed August 2022).

Relevance of Distribution to Status. Geographic and depth distributions were the key spatial factors considered in determining the status of coral species and in the listing of *M. australiensis* in 2014. A narrow geographic or depth distribution exacerbates a species' extinction risk because larger proportions of the population are likely to be exposed to any single disturbance. In contrast, a broad overall distribution moderates a species' extinction risk because the population is distributed across a range of geographic areas and depths, and thus lower proportions of the populations are likely to be exposed to any single disturbance (79 FR 53851).

4.12.3. Abundance

Relative Abundance: DeVantier and Turak (2017) characterized abundances of over 600 Indo-Pacific reef-building coral species in 31 Veron ecoregions from the Red Sea to Fiji, as further described in Section 4.1.3 above. *Montipora australiensis* was recorded in 4 of the 31 ecoregions. Within those 4 ecoregions, it had a mean overall abundance of 4.68 (Uncommon), ranging from 0.67 (Rare) in the Sulu Sea Ecoregion to 9.71 (Uncommon) in the Sunda Shelf Ecoregion. The mean overall abundance of *M. australiensis* for all 31 ecoregions was 0.59 (Rare, DeVantier and Turak 2017, Table S2), and most of the 27 ecoregions where it was not recorded appear to be within its range. The Coral Traits Database (https://coraltraits.org/, accessed August 2022) lists *M. australiensis*'s abundance estimate on the GBR as "rare," but does not cite DeVantier and Turak

(2017). Within its range, the relative abundance of *M. australiensis* may vary locally from very rare to at least uncommon. However, based on the above information, the rangewide relative abundance of *M. australiensis* is rare to uncommon. Thus, current information indicates that *M. australiensis* has a higher relative abundance (rare to uncommon) than we were aware of at the time of listing in 2014 (rare).

Absolute Abundance. Absolute abundance is an estimate of the total number of colonies of a species that currently exist throughout its range. Based on *M. australiensis'*s distribution and relative abundance, NMFS (2014) estimated the absolute abundance of *M. australiensis* to be at least millions of colonies. Dietzel et al. (2021) estimated its absolute abundance at 30.5 million colonies. Muir et al. (2022) argued that the data were unsuitable to provide such quantitative estimates, and Dietzel et al.'s (2022) reply agreed that better data are needed. Based on the updated information *M. australiensis'*s absolute abundance is likely to be at least tens of millions of colonies. Thus, current information indicates that *M. australiensis* has a higher absolute abundance (at least tens of millions) than we were aware of at the time of listing in 2014 (at least millions).

Abundance Trends. As described above in the general Threats Evaluation and below for threats to *M. australiensis*, the most important threats (i.e., ocean warming, ocean acidification) have worsened since 2014, and substantial impacts to *Montipora* species have occurred, although no species-specific data are available for *M. australiensis*. Based on the continued worsening in the most important threats, it is likely that *M. australiensis* is decreasing in overall abundance (i.e., abundance across all the ecoregions that make up its range).

Relevance of Abundance to Status. Abundance is the key demographic factor considered in determining the status of coral species and in the listing of *M. australiensis* in 2014. A low relative or absolute abundance, especially in combination with declining abundance, exacerbates a species' extinction risk because larger proportions of the population are likely to be exposed to any single disturbance. In contrast, a higher relative or absolute abundance moderates a species' extinction risk because lower proportions of the population are likely to be exposed to any single disturbance (79 FR 53851). Since the relative abundance and absolute abundance of *M. australiensis* are both greater than we were aware of at the time of listing in 2014, its abundance may have a greater capacity to moderate extinction risk.

4.12.4. Threats

This section provides an updated threats evaluation for *M. australiensis*, focusing on the threats that contributed to its listing (79 FR 53851), including ocean warming, ocean acidification, disease, fishing, LBSP, predation, and inadequacy of existing regulatory mechanisms. In addition, current information indicates that collection and trade is also impacting the status of the species. A threats summary table is provided, including relative importance ratings for the threats, effects of threats since listing in 2014, and projected effects of threats in the foreseeable future.

Ocean Warming: As noted in Section 3.2.1 above, since listing in 2014, the effects of ocean warming on Indo-Pacific reef-building corals in general have substantially worsened. In response to the 2014–2017 series of warming-induced bleaching events, *Montipora* corals were generally among the most impacted coral taxa in different locations around the Indo-Pacific (e.g., Frade et al 2018, Fox et al. 2019, McClanahan et al. 2020, Gilmour et al. 2022). In a study of the changes in the GBR's coral communities, which is within *M. australiensis*'s range, between 1995/96 and 2016/17, Dietzel et al. (2020) found that *Montipora* species declined by 72.1% on the reef crest and 35.3% on the reef slope (6–7 m depth). Section 3.2.1 also describes how ocean warming is projected to greatly worsen in the foreseeable future (i.e., between now and 2100). In conclusion, the current information indicates that *M. australiensis* continues to be highly susceptible to ocean warming, that this threat has substantially worsened since listing in 2014, and that it will greatly worsen in the foreseeable future (Table 15).

Ocean Acidification: As noted in Section 3.2.2 above, since listing in 2014, the effects of ocean acidification on Indo-Pacific reef-building corals have worsened. Generally, *Montipora* species are susceptible to reduced calcification and skeletal growth from ocean acidification (Brainard et al. 2011, 79 FR 53851, Evenson et al. 2021). Section 3.2.2 also describes how ocean acidification is projected to greatly worsen in the foreseeable future. In conclusion, the current information indicates that *M. australiensis* continues to be susceptible to ocean acidification, that this threat has worsened since listing in 2014, and that it will greatly worsen in the foreseeable future (Table 15).

Disease: As noted in Section 3.2.3 above, since listing in 2014, the effects of disease on Indo-Pacific corals have increased, mainly in response to the 2014–2017 bleaching events. Generally, *Montipora* species are susceptible to most of the diseases that infect coral, and are commonly affected by acute and lethal diseases (Brainard et al. 2011, 79 FR 53851, Aeby et al. 2016, Das et al. 2022). Section 3.2.3 also describes how disease is projected to substantially worsen in the foreseeable future. In conclusion, the current information indicates that *M. australiensis* continues to be susceptible to disease, that this threat has worsened since listing in 2014, and that it will substantially worsen in the foreseeable future (Table 15).

Fishing: As noted in Section 3.2.4 above, since listing in 2014, the direct and indirect effects of fishing on Indo-Pacific corals have continued, likely intensifying in some locations while lessening in others due to various factors. Generally, columnar corals such as *M. australiensis* may be more susceptible than other corals to damage by fishing gear because of their morphology (Brainard et al. 2011, 79 FR 53851). Section 3.2.4 also describes how fishing is projected to substantially worsen in the foreseeable future. In conclusion, the current information indicates that *M. australiensis* continues to be susceptible to fishing, that this threat has continued since listing in 2014, and that it will substantially worsen in the foreseeable future (Table 15).

LBSP: As noted in Section 3.2.5 above, since listing in 2014, the effects of LBSP on Indo-Pacific corals have continued, likely intensifying in some locations while lessening in others due to various factors. Generally, *Montipora* species are moderately susceptible to sediment and nutrients, compared to other reef-building coral taxa (Brainard et al. 2011, 79 FR 53851, Carlson at al. 2019). Section 3.2.5 also describes how LBSP is projected to substantially worsen in the foreseeable future. In conclusion, the current information indicates that *M. australiensis* continues to be susceptible to LBSP, that this threat has continued since listing in 2014, and that it will substantially worsen in the foreseeable future (Table 15).

Predation: As noted in Section 3.2.6 above, since listing in 2014, the effects of predation on Indo-Pacific corals have increased, mainly because the 2014–2017 bleaching events resulted in more favorable conditions for predators such as COTS. Generally, *Montipora* species are susceptible to predation (Brainard et al. 2011, 79 FR 53851, Tkachenko and Huang 2022). Section 3.2.6 also describes how predation is projected to substantially worsen in the foreseeable future. In conclusion, the current information indicates that *M. australiensis* continues to be susceptible to predation, that this threat has worsened since listing in 2014, and that it will substantially worsen in the foreseeable future (Table 15).

Collection and Trade: Although collection and trade did not contribute to the listing of *M. australiensis* (79 FR 53851), the following information indicates that this threat is likely impacting the status of the species. As noted in Section 3.2.7 above, since listing in 2014, the effects of collection and trade on Indo-Pacific corals have continued. According to the CITES database cited in Section 3.2.7, since 2006, over 100,000 *Montipora* units were globally imported and exported annually. These units were not identified to species, thus may have included an undeterminable number of unidentified *M. australiensis*. In addition, the database also records that in 2015 and 2017, a few dozen *M. australiensis* units were globally imported and exported annually (NMFS 2022a). Because of the ongoing and projected growth in the industry, collection and trade may increasingly impact the status of *M. australiensis*. Section 3.2.7 also describes how collection and trade is projected to substantially worsen in the foreseeable future. In conclusion, the current information indicates that *M. australiensis* is susceptible to collection and trade, that this threat has continued since listing in 2014, and that it will substantially worsen in the foreseeable future (Table 15).

Sea-level Rise: As noted in Section 3.2.8 above, since listing in 2014, sea-level rise has likely been too gradual to result in measurable effects on Indo-Pacific reef-building corals. In those cases where earthquakes have resulted in substrate uplift resembling sea-level rise, these substrates have been colonized by rapidly-growing corals like *Montipora* species. In conclusion, as in the final rule, the current information indicates that *M. australiensis* is not susceptible to sea-level rise, that there have been no detectable trends in the effects of this threat since listing in 2014, but that it will worsen in the foreseeable future (Table 15).

Regulatory Mechanisms: As noted in Section 3.2.9 above, since listing in 2014, some progress has been made with GHG management as well as controlling local threats although existing regulatory mechanisms are still inadequate to control any of the threats. Section 3.2.9 also describes how it is unlikely that regulatory mechanisms will be improved to the point where they are adequate to control any of the threats in the foreseeable future. In conclusion, the current information indicates that existing regulatory mechanisms remain inadequate to control any threat to *M. australiensis*, and that improvement is unlikely in the foreseeable future (Table 15).

Threats Conclusion for *M. australiensis*: Since *M. australiensis* was listed in 2014, many of the threats to the species have worsened. All threats are projected to worsen in the foreseeable future, with the possible exception of regulatory mechanisms, which may continue to improve but also are likely to remain inadequate for controlling any of the threats (Table 15).

Although the final rule rated the relative importance of threats to the world's reef-building corals (Table 2), it did not apply those ratings to *M. australiensis* (79 FR 53851). Instead, the final rule concluded that *M. australiensis* is highly susceptible to ocean warming, and susceptible to ocean acidification, disease, fishing, LBSP, and predation, while regulatory mechanisms were inadequate for controlling any threat (79 FR 53851). However, as summarized above, we now have more genus-specific and species-specific information available on the importance of each threat to *Montipora* species and *M. australiensis*, respectively. Based on the general importance ratings of the threats to Indo-Pacific reef-building corals (Table 3) and the genus-specific and species-specific information above, we conclude that the relative importance ratings of each threat to Indo-Pacific corals apply to *M. australiensis*. In addition, the observed threat trends since 2014 and projected threat trends in the foreseeable future are provided (Table 15).

Table 15. Summary of threats evaluation for *M. australiensis*. For each threat, relative importance to the extinction risk of the species, observed trend since 2014, and projected trend in the foreseeable future are provided.

Threat (listing factor)	**Importance**	**Observed Trend in Effects Since 2014**	**Projected Trend in Effects to 2100**
Ocean Warming (Factor E)	Very High	Substantially worsened	Greatly worsen
Ocean Acidification (Factor E)	High	Worsened	Greatly worsen
Disease (Factor C)	High	Worsened	Substantially worsen
Fishing (Factor A)	Medium	Continued	Substantially worsen
LBSP (Factors A and E)	Low-Medium	Continued	Substantially worsen
Predation (Factor C)	Low-Medium	Worsened	Substantially worsen
Collection and Trade (Factor B)	Low-Medium	Continued	Substantially worsen
Sea-level Rise (Factor E)	Low	No detectable trends	Worsen
Inadequacy of Existing Regulatory Mechanisms (Factor D)	High	Some improvement but still inadequate	Improvement but likely still inadequate

4.12.5. Conclusion

As explained in the 2014 final listing rule (79 FR 53851), a species' vulnerability to extinction results from the combination of its spatial (i.e., distribution) and demographic (i.e., abundance) characteristics, threat susceptibilities, and consideration of the baseline environment and future projections of threats. *Montipora australiensis* was listed as threatened in 2014 because of its geographic distribution restricted to parts of the Coral Triangle and western Indian Ocean, low abundance, high susceptibility to ocean warming, susceptibilities to ocean acidification, fishing, LBSP, disease, and predation, inadequate regulatory mechanisms, declining baseline conditions, and projected worsening of threats (79 FR 53851).

Since 2014, we have learned that *M. australiensis* has: (1) higher relative abundance (rare to uncommon instead of rare); and (2) higher absolute abundance (at least tens of millions of colonies instead of at least millions of colonies). That is, *M. australiensis* is more abundant than we believed in 2014, and thus may have a higher capacity to moderate the effects of the threats, as explained in the Relevance of Abundance to Status section above.

Since 2014, the effects of ocean warming have substantially worsened, and the effects of most other threats have worsened as well. All threats are projected to substantially worsen under current global GHG regulatory mechanisms, which would result in global warming of 2.6–3.4°C above the pre-industrial baseline by 2100 (see Fig. 4 in Section 3.1 above). Even if the goal of the Paris Agreement is achieved (i.e., limiting global warming to 1.5°C above pre-industrial by 2100), the threats would become much worse than they are currently (Dixon et al. 2022), likely preventing the recovery of *M. australiensis*. Current regulatory mechanisms are grossly inadequate, especially GHG management.

In conclusion, the above information shows that *M. australiensis* is more abundant than we believed in 2014, but that the threats have worsened and that collection and trade is also an important threat to the species. Especially concerning is that the most important threat to the species, ocean warming, has substantially worsened since the species was listed in 2014. The other important threats to the species, including ocean acidification, disease, fishing, LBSP, predation, and collection and trade have also either worsened or continued since 2014. While there has been some progress with regulatory mechanisms, primarily because of the 2016 Paris Agreement, regulatory mechanisms for both global and local threats are still inadequate. However, the species' abundance is higher than we were aware of at the time of listing in 2014, which is a key factor for moderating threats.

4.13. *Pavona diffluens* (Lamarck 1816)

4.13.1. Biology

Taxonomy. *Pavona diffluens* was described by Lamarck (1816). It is included in the Corals of the World books (Veron 2000) and website (http://www.coralsoftheworld.org/, accessed August 2022), and is accepted by WoRMS (Hoeksma and Cairns 2021). Colonies similar to *P. diffluens* from the Pacific are considered a separate, undescribed species (Veron and Pichon 1980, Veron 2014). This species was listed in 2014 based on the assumption that its range is limited to the Indian Ocean (79 FR 53851).

Morphology. Colonies are lumpy with deep corallite centers, and are tan in color (Fig. 29, Veron et al. 2016, Fenner 2020a).

Figure 29. *Pavona diffluens*, showing colony and branch morphology. Both photos from the Red Sea (Charlie Veron; Veron et al. 2016).

Habitat. *Pavona diffluens* occurs in at least upper reef slopes, mid-slopes, lower reef crests, reef fats, and lagoons (79 FR 53851). The Coral Traits Database (https://coraltraits.org/, accessed August 2022) lists *P. diffluens*'s water clarity preference as "clear", and wave exposure preference as "broad".

Life History. Little is known of the life history of *P. diffluens*, although other *Pavona* species are gonochoric broadcast spawners. Broadcast spawners release both male and female gametes into the water column and fertilization takes place externally. Larvae settle on suitable substrates such as rock or dead coral and grow into colonies (79 FR 53851).

4.13.2. Distribution

Geographic Distribution. *Pavona diffluens* has a limited geographic distribution, occurring in only nine MEOWs (Fig. 30), and does not occur in U.S. waters based on information in NMFS (2022c). Colonies similar to *P. diffluens* from the Pacific are considered a separate, undescribed species (79 FR 53851, Veron 2014) and the species does not occur in U.S. waters. Its distribution is restricted to parts of the western Indian Ocean along coastal East Africa, the Red Sea, the Gulf of Oman, and the Chagos Islands, where localized human impacts are high for coral reefs over the 21st century. In addition, parts of the Red Sea are projected to experience severe impacts from climate change more rapidly than other parts of the Indo-Pacific region. The current information indicates that *P. diffluens* occurs in one more MEOW than we were aware of at the time of listing in 2014, the Chagos Islands (NMFS 2022c).

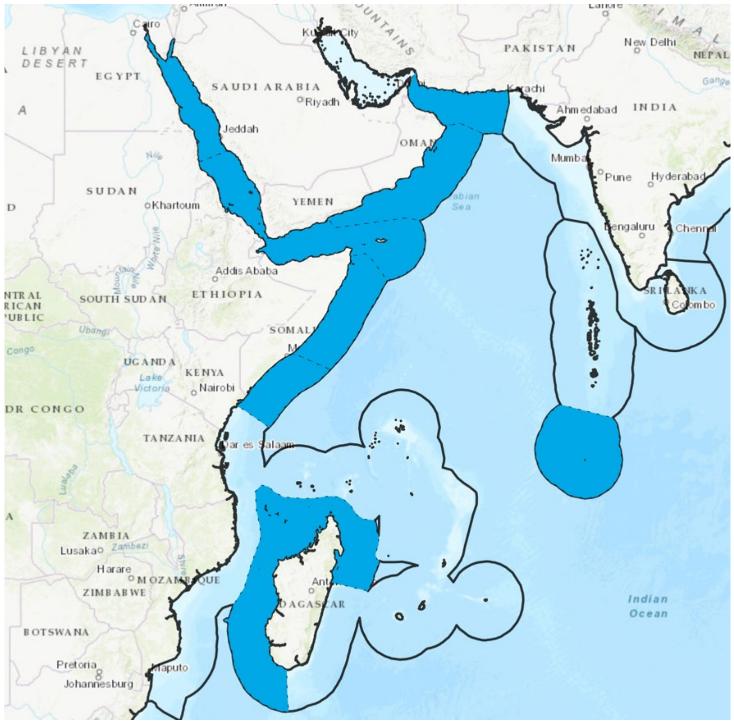


Figure 30. Geographic distribution of *P. diffluens*.

Depth Distribution. *Pavona diffluens* occurs at depths of approximately 5–20 m (79 FR 53851, Coral Traits Database https://coraltraits.org/, accessed August 2022).

Relevance of Distribution to Status. Geographic and depth distributions were the key spatial factors considered in determining the status of coral species and in the listing of *P. diffluens* in 2014. A narrow geographic or depth distribution exacerbates a species' extinction risk because larger proportions of the population are likely to be exposed to any single disturbance. In contrast, a broad overall distribution moderates a species' extinction risk because the population is distributed across a range of geographic areas and depths, and thus lower proportions of the populations are likely to be exposed to any single disturbance. For example, one reason that *P. diffluens* was listed was because of its restricted geographic distribution (79 FR 53851). Since the geographic distribution of *P. diffluens* is greater than we were aware of at the time of listing in 2014, its distribution has a greater capacity to moderate extinction risk.

4.13.3. Abundance

Relative Abundance: DeVantier and Turak (2017) characterized abundances of over 600 Indo-Pacific reef-building coral species in 31 Veron ecoregions from the Red Sea to Fiji, as further described in Section 4.1.3 above. *Pavona diffluens* was recorded in 4 of the 31 ecoregions. Within those 4 ecoregions, it had a mean overall abundance of 4.88 (Uncommon), ranging from 1.08 (Uncommon) in the Socotra Archipelago Ecoregion to 11.03 (Common) in the Red Sea North-central Ecoregion. The mean overall abundance of *P. diffluens* for all 31 ecoregions was 0.65 (Rare, DeVantier and Turak 2017, Table S2), however most of the 27 ecoregions where it was not recorded appear to be outside its range. The Coral Traits Database (https://coraltraits.org/, accessed August 2022) lists *P. diffluen*'s global abundance estimate as "uncommon," but does not cite DeVantier and Turak (2017). Within its range, the relative abundance of *P. diffluens* may vary locally from very rare to at least common. However, based on the above information, the rangewide relative abundance of *P. diffluens* is uncommon.

Absolute Abundance. Absolute abundance is an estimate of the total number of colonies of a species that currently exist throughout its range. Based on *P. diffluen'*s distribution and relative abundance, NMFS (2014) estimated the absolute abundance of *P. diffluens* to be at least millions of colonies. Based on current information, no changes to that estimate are warranted.

Abundance Trends. As described above in the general Threats Evaluation and below for threats to *P. diffluens*, the most important threats (i.e., ocean warming, ocean acidification) have worsened since 2014, and substantial impacts to *Pavona* species have occurred, although no species-specific data are available for *P. diffluens*. Based on the continued worsening in the most important threats, it is likely that *P. diffluens* is decreasing in overall abundance (i.e., abundance across all the ecoregions that make up its range).

Relevance of Abundance to Status. Abundance is the key demographic factor considered in determining the status of coral species and in the listing of *P. diffluens* in 2014. A low relative or absolute abundance, especially in combination with declining abundance, exacerbates a species' extinction risk because larger proportions of the population are likely to be exposed to any single disturbance. In contrast, a higher relative or absolute abundance moderates a species' extinction risk because lower proportions of the population are likely to be exposed to any single disturbance (79 FR 53851).

4.13.4. Threats

This section provides an updated threats evaluation for *P. diffluens*, focusing on the threats that contributed to its listing (79 FR 53851), which included ocean warming, ocean acidification, disease, fishing, LBSP, predation, and inadequacy of existing regulatory mechanisms. A threats summary table is provided, including relative importance ratings for the threats, effects of threats since listing in 2014, and projected effects of threats in the foreseeable future.

Ocean Warming: As noted in Section 3.2.1 above, since listing in 2014, the effects of ocean warming on Indo-Pacific reef-building corals in general have substantially worsened. In response to the 2014–2017 series of warming-induced bleaching events, *Pavona* corals were among the most impacted coral taxa in some locations (e.g., Vo et al. 2020) but the least impacted in others (McClanahan et al. 2020). Section 3.2.1 also describes how ocean warming is projected to greatly worsen in the foreseeable future (i.e., between now and 2100). In conclusion, the current information indicates that *P. diffluens* continues to be susceptible to ocean warming, that this threat has substantially worsened since listing in 2014, and that it will greatly worsen in the foreseeable future (Table 16).

Ocean Acidification: As noted in Section 3.2.2 above, since listing in 2014, the effects of ocean acidification on Indo-Pacific reef-building corals have worsened. In other *Pavona* species, laboratory studies have shown impacts of low pH on calcification (Brainard et al. 2011, 79 FR 53851, Godefroid et al. 2021), and a field study showed that *Pavona* species had high bioerosion rates in the eastern Pacific (Cosain-Díaz et al. 2021). Section 3.2.2 also describes how ocean acidification is projected to greatly worsen in the foreseeable future. In conclusion, the current information indicates that *P. diffluens* continues to be susceptible to ocean acidification, that this threat has worsened since listing in 2014, and that it will greatly worsen in the foreseeable future (Table 16).

Disease: As noted in Section 3.2.3 above, since listing in 2014, the effects of disease on Indo-Pacific corals have increased, mainly in response to the 2014–2017 bleaching events. Generally, *Pavona* corals are thought to have some susceptibility to disease (79 FR 53851). Section 3.2.3 also describes how disease is projected to substantially worsen in the foreseeable future. In conclusion, the current information indicates that *P. diffluens* continues to be susceptible to disease, that this threat has worsened since listing in 2014, and that it will substantially worsen in the foreseeable future (Table 16).

Fishing: As noted in Section 3.2.4 above, since listing in 2014, the direct and indirect effects of fishing on Indo-Pacific corals have continued, likely intensifying in some locations while lessening in others due to various factors (Brainard et al. 2011, 79 FR 53851). Generally, *Pavona* corals are thought to have some susceptibility to fishing (79 FR 53851). Section 3.2.4 also describes how fishing is projected to substantially worsen in the foreseeable future. In conclusion, the current information indicates that *P. diffluens* continues to be susceptible to fishing, that this threat has continued since listing in 2014, and that it will substantially worsen in the foreseeable future (Table 16).

LBSP: As noted in Section 3.2.5 above, since listing in 2014, the effects of LBSP on Indo-Pacific corals have continued, likely intensifying in some locations while lessening in others due to various factors. Generally, *Pavona* species are thought to have some susceptibility to sediment and nutrients (Brainard et al. 2011, 79 FR 53851). Section 3.2.5 also describes how LBSP is projected to substantially worsen in the foreseeable future. In conclusion, the current information indicates that *P. diffluens* continues to be susceptible to LBSP, that this threat has continued since listing in 2014, and that it will substantially worsen in the foreseeable future (Table 16).

Predation: As noted in Section 3.2.6 above, since listing in 2014, the effects of predation on Indo-Pacific corals have increased, mainly because the 2014–2017 bleaching events resulted in more favorable conditions for predators such as COTS. Generally, *Pavona* corals are thought to have some susceptibility to predation (79 FR 53851). Section 3.2.6 also describes how predation is projected to substantially worsen in the foreseeable future. In conclusion, the current information indicates that *P. diffluens* continues to be susceptible to predation, that this threat has worsened since listing in 2014, and that it will substantially worsen in the foreseeable future (Table 16).

Collection and Trade: As noted in Section 3.2.7 above, since listing in 2014, the effects of collection and trade on Indo-Pacific corals have continued. According to the CITES database cited in Section 3.2.7, since 1986, tens of thousands of *Pavona* units were globally imported and exported annually. These units were not identified to species, thus may have included an undeterminable number of unidentified *P. diffluens*. However, the database had no records of *P. diffluens* (NMFS 2022a) and there is no other information to indicate that *P. diffluens* is particularly targeted for collection and trade. While Section 3.2.7 describes how collection and trade is projected to substantially worsen in the foreseeable future (Table 16), the current information does not indicate that collection and trade is a threat to *P. diffluens*. Thus, we conclude that collection and trade has lower relative importance to the extinction risk of *P. diffluens* (i.e., Low instead of Low-Medium) than for most of the other listed species.

Sea-level Rise: As noted in Section 3.2.8 above, since listing in 2014, sea-level rise has likely been too gradual to result in measurable effects on Indo-Pacific reef-building corals. In those cases where earthquakes have resulted in substrate uplift resembling sea-level rise, these substrates have been colonized by corals. In conclusion, as in the final rule, the current information indicates that *P.*

diffluens is not susceptible to sea-level rise, that there have been no detectable trends in the effects of this threat since listing in 2014, but that it will worsen in the foreseeable future (Table 16).

Regulatory Mechanisms: As noted in Section 3.2.9 above, since listing in 2014, some progress has been made with GHG management as well as controlling local threats although existing regulatory mechanisms are still inadequate to control any of the threats. Section 3.2.9 also describes how it is unlikely that regulatory mechanisms will be improved to the point where they are adequate to control any of the threats in the foreseeable future. In conclusion, the current information indicates that existing regulatory mechanisms remain inadequate to control any threat to *P. diffluens*, and that improvement is unlikely in the foreseeable future (Table 16).

Threats Conclusion for *P. diffuens*: Since *P. diffluens* was listed in 2014, many of the threats to the species have worsened. All threats are projected to worsen in the foreseeable future, with the possible exception of regulatory mechanisms, which may continue to improve but also are likely to remain inadequate for controlling any of the threats (Table 16).

Although the final rule rated the relative importance of threats to the world's reef-building corals (Table 2), it did not apply those ratings to *P. diffluens* (79 FR 53851). Instead, the final rule concluded that *P. diffluens* is susceptible to ocean warming, ocean acidification, disease, fishing, LBSP, and predation, while regulatory mechanisms were inadequate for controlling any threat (79 FR 53851). However, as summarized above, we now have more genus-specific and species-specific information available on the importance of each threat to *Pavona* species and *P. diffluens*, respectively. Based on the general importance ratings of the threats to Indo-Pacific reef-building corals (Table 3) and the genus-specific and species-specific information above, we conclude that the relative importance ratings of each threat to Indo-Pacific corals apply to *P. diffluens*, with the exception of collection and trade (now rated as Low instead of Low-Medium). In addition, the observed threat trends since 2014 and projected threat trends in the foreseeable future are provided (Table 16).

Table 16. Summary of threats evaluation for *P. diffluens*. For each threat, relative importance to the extinction risk of the species, observed trend since 2014, and projected trend in the foreseeable future are provided.

Threat (listing factor)	**Importance**	**Observed Trend in Effects Since 2014**	**Projected Trend in Effects to 2100**
Ocean Warming (Factor E)	Very High	Substantially worsened	Greatly worsen
Ocean Acidification (Factor E)	High	Worsened	Greatly worsen
Disease (Factor C)	High	Worsened	Substantially worsen
Fishing (Factor A)	Medium	Continued	Substantially worsen
LBSP (Factors A and E)	Low-Medium	Continued	Substantially worsen
Predation (Factor C)	Low-Medium	Worsened	Substantially worsen
Collection and Trade (Factor B)	Low	Continued	Substantially worsen
Sea-level Rise (Factor E)	Low	No detectable trends	Worsen
Inadequacy of Existing Regulatory Mechanisms (Factor D)	High	Some improvement but still inadequate	Improvement but likely still inadequate

4.13.5. Conclusion

As explained in the 2014 final listing rule (79 FR 53851), a species' vulnerability to extinction results from the combination of its spatial (i.e., distribution) and demographic (i.e., abundance) characteristics, threat susceptibilities, and consideration of the baseline environment and future projections of threats. *Pavona diffluens* was listed as threatened in 2014 because of its restricted geographic distribution, low abundance, susceptibilities to ocean warming, ocean acidification, fishing, LBSP, disease, and predation, inadequate regulatory mechanisms, declining baseline conditions, and projected worsening of threats (79 FR 53851).

Since 2014, we have learned that *P. diffluens* has a broader geographic distribution (nine MEOWs instead of eight) than indicated in the final listing rule (79 FR 53851). While its geographic distribution is only one MEOW greater, the addition of that MEOW (Chagos Islands) means that its geographic distribution is not limited to east Africa and the Red Sea but rather extends into the central Indian Ocean. That is, *P. diffluens* is more broadly distributed than we believed in 2014, and thus may have a higher capacity to moderate the effects of the threats, as explained in the Relevance of Distribution to Status section above.

Since 2014, the effects of ocean warming have substantially worsened, and the effects of most other threats have worsened as well. All threats are projected to substantially worsen under current global GHG regulatory mechanisms, which would result in global warming of 2.6–3.4°C above the pre-industrial baseline by 2100 (see Fig. 4 in Section 3.1 above). Even if the goal of the Paris Agreement is achieved (i.e., limiting global warming to 1.5°C above pre-industrial by 2100), the threats would become much worse than they are currently (Dixon et al. 2022), likely preventing the recovery of *P. diffluens*. Current regulatory mechanisms are grossly inadequate, especially GHG management.

In conclusion, the above information shows that *P. diffluens* is more broadly distributed than we believed in 2014, but that the threats have worsened. Especially concerning is that the most important threat to the species, ocean warming, has substantially worsened since the species was listed in 2014. The other important threats to the species, including ocean acidification, disease, fishing, LBSP, and predation have also either worsened or continued since 2014. While there has been some progress with regulatory mechanisms, primarily because of the 2016 Paris Agreement, regulatory mechanisms for both global and local threats are still inadequate. However, the species' distribution is broader than we were aware of at the time of listing in 2014, which is a key factor for moderating threats.

4.14. *Porites napopora* (Veron 2000)

4.14.1. Biology

<u>Taxonomy</u>. *Porites napopora* was one the new species described in the Corals of the World books (Veron 2000), with additional details provided in Veron (2002). It is included in the Corals of the World website (http://www.coralsoftheworld.org/, accessed August 2022), and is accepted by WoRMS (Hoeksma and Cairns 2021).

<u>Morphology</u>. Colonies form thin plates with cylindrical, tapering branches going in various directions. Corallites are recessed deeply between ridges. Colonies are brown with white corallite centers, making colonies look spotted (Fig. 31, Veron et al. 2016).

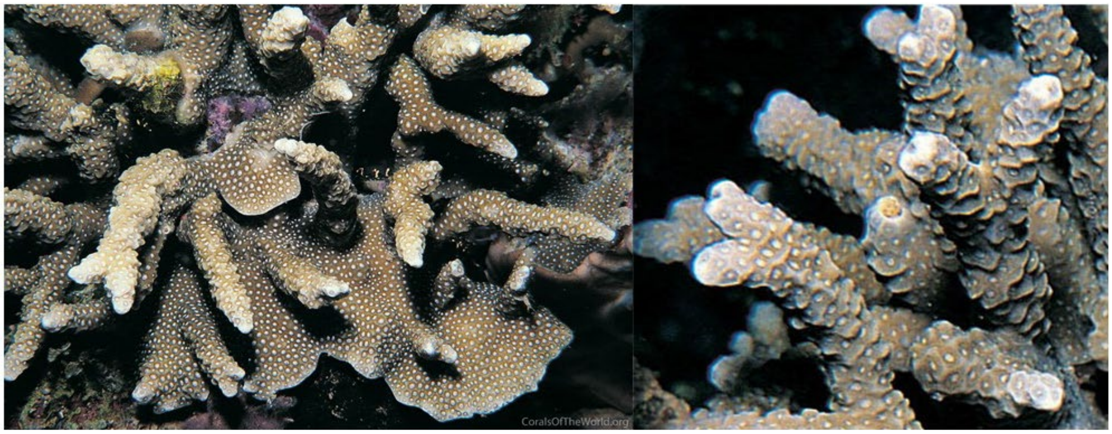


Figure 31. *Porites napopora*, showing colony and branch morphology. Both photos from Indonesia (Charlie Veron, Veron et al., 2016).

Habitat. *Porites napopora* occurs in shallow reef habitats either protected from wave action or exposed to moderate wave surge (Veron 2002). The Coral Traits Database (https://coraltraits.org/, accessed August 2022) lists *P. napopora*'s water clarity preference as "clear," and wave exposure preference as "broad."

Life History. The life history of *P. napopora* has not been studied. Generalizations cannot be made based on other Indo-Pacific *Porites* species because of their high diversity of general life histories (e.g., the 7 Indo-Pacific *Porites* species in Darling et al. 2012 are competitive, weedy, or stress-tolerant) and reproductive life histories (e.g., the 14 Indo-Pacific *Porites* species in Baird et al. 2009 are gonochoric broadcast spawners or gonochoric brooders) within the genus. Furthermore, susceptibilities to threats often differ between branching *Porites* species such as *P. napopora* and massive *Porites* species (Brainard et al. 2011, 79 FR 53851).

4.14.2. Distribution

Geographic Distribution. *Porites napopora* has a relatively limited geographic distribution, occurring in 19 MEOWs (Fig. 32), and does not occur in U.S. waters based on information in NMFS (2022c). Its distribution is limited to parts of the Coral Triangle and the western equatorial Pacific Ocean. Despite the large number of islands and environments that are included in the species' range, it is mostly limited to an area projected to have the most rapid and severe impacts from climate change and localized human impacts for coral reefs over the 21st century.

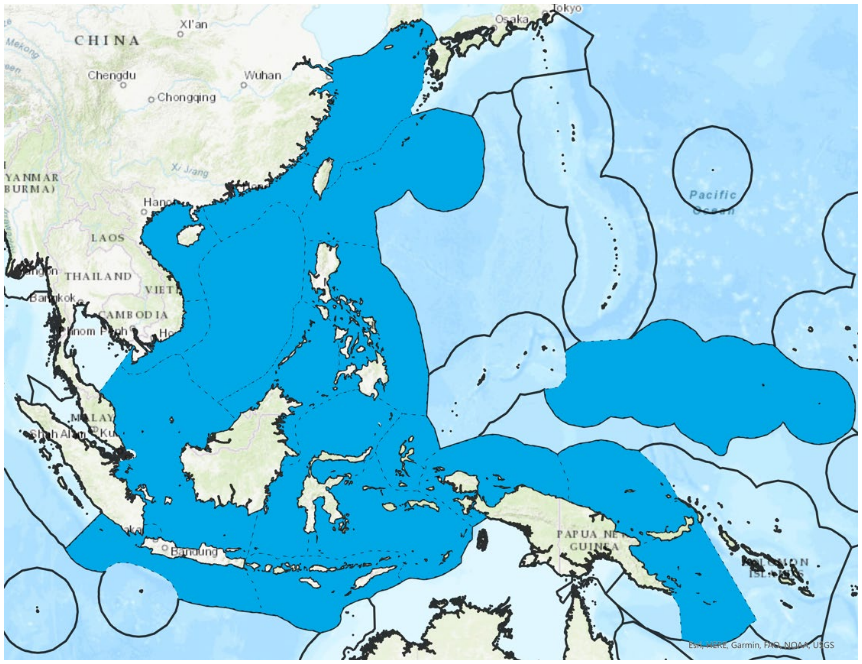


Figure 32. Geographic distribution of *P. napopora*.

Depth Distribution. *Porites napopora* has a relatively moderate depth range, occurring at depths of 3–17 m (Coral Traits Database https://coraltraits.org/, accessed August 2022, Scaps et al. 2007). Thus, current information indicates that *P. napopora* has a slightly greater depth range (3– 17 m) than we were aware of at the time of listing in 2014 (3–15 m).

Relevance of Distribution to Status. Geographic and depth distributions were the key spatial factors considered in determining the status of coral species and in the listing of *P. napopora* in 2014. A narrow geographic or depth distribution exacerbates a species' extinction risk because larger proportions of the population are likely to be exposed to any single disturbance. In contrast, a broad overall distribution moderates a species' extinction risk because the population is distributed across a range of geographic areas and depths, and thus lower proportions of the populations are likely to be exposed to any single disturbance. For example, one reason that *P. napopora* was listed was because of its narrow depth distribution of 3–15 m (79 FR 53851).

4.14.3. Abundance

Relative Abundance. DeVantier and Turak (2017) characterized abundances of over 600 Indo-Pacific reef-building coral species in 31 Veron ecoregions from the Red Sea to Fiji, as further described in Section 4.1.3 above. *Porites napopora* was recorded in 9 of the 31 ecoregions. Within those 9 ecoregions, it had a mean overall abundance of 19.32 (Common), ranging from 2.50 (Uncommon) in the Celebes Sea Ecoregion to 71.21 (Very Common) in the Cenderawasih Bay, Papua Ecoregion. The mean overall abundance of *P. napopora* for all 31 ecoregions was 5.46 (Uncommon, DeVantier and Turak 2017, Table S2), however some of the 22 ecoregions where it was not recorded may be outside its range. The Coral Traits Database (https://coraltraits.org/, accessed August 2022) lists *P. napopora*'s global abundance estimate as "uncommon," but does not cite DeVantier and Turak (2017). Within its range, the relative abundance of *P. napopora* may vary locally from very rare to at least very common. However, based on the above information, the rangewide relative abundance of *P. napopora* is uncommon to common. Thus, current information indicates that *A. globiceps* has a higher relative abundance (uncommon to common) than we were aware of at the time of listing in 2014 (rare to uncommon).

Absolute Abundance. Absolute abundance is an estimate of the total number of colonies of a species that currently exist throughout its range. Based on *P. napopora's* distribution and relative abundance, NMFS (2014) estimated the absolute abundance of *P. napopora* to be at least millions of colonies. Based on current information, no changes to that estimate are warranted.

Abundance Trends. As described above in the general Threats Evaluation and below for threats to *P. napopora*, the most important threat (i.e., ocean warming) has worsened since 2014, and substantial impacts to *Porites* species have occurred, although no species-specific data are available for *P. napopora*. Based on the continued worsening in the most important threats, it is likely that *P. napopora* is decreasing in overall abundance (i.e., abundance across all the ecoregions that make up its range).

Relevance of Abundance to Status. Abundance is the key demographic factor considered in determining the status of coral species and in the listing of *P. napopora* in 2014. A low relative or absolute abundance, especially in combination with declining abundance, exacerbates a species' extinction risk because larger proportions of the population are likely to be exposed to any single disturbance. In contrast, a higher relative or absolute abundance moderates a species' extinction risk because lower proportions of the population are likely to be exposed to any single disturbance (79 FR 53851). Since the relative abundance of *P. napopora* is greater than we were aware of in at the time of listing in 2014, its abundance may have a greater capacity to moderate extinction risk.

4.14.4. Threats

This section provides an updated threats evaluation for *P. napopora*, focusing on the threats that contributed to its listing (79 FR 53851), which included ocean warming, disease, fishing, LBSP, and inadequacy of existing regulatory mechanisms. In addition, current information indicates that ocean acidification and predation are likely to be impacting the status of the species. A threats summary table is provided, including relative importance ratings for the threats, effects of threats since listing in 2014, and projected effects of threats in the foreseeable future.

Ocean Warming: As noted in Section 3.2.1 above, since listing in 2014, the effects of ocean warming on Indo-Pacific reef-building corals in general have substantially worsened. In response to the 2014–2017 series of warming-induced bleaching events, *Porites* corals were among the most impacted coral taxa in some locations around the Indo-Pacific (e.g., Fox et al. 2019, Vargas-Angel et al. 2019, Vo et al. 2020), especially branching *Porites* species (McClanahan et al. 2020, Gilmour et al. 2022). Section 3.2.1 also describes how ocean warming is projected to greatly worsen in the foreseeable future (i.e., between now and 2100). In conclusion, the current information indicates that *P. napopora* continues to be susceptible to ocean warming, that this threat has substantially worsened since listing in 2014, and that it will greatly worsen in the foreseeable future (Table 17).

Ocean Acidification: As noted in Section 3.2.2 above, since listing in 2014, the effects of ocean acidification on Indo-Pacific reef-building corals have worsened. In studies of coral community composition in naturally low pH environments, *Porites* corals have been some of the most abundant taxa (Barkley et al. 2015, Camp et al. 2019). However, recent studies demonstrate negative impacts of ocean acidification on *Porites* skeletal growth (Mollica et al. 2018, Guo et al. 2020, Kang et al. 2021) and recruitment (Smith et al. 2020). Section 3.2.2 also describes how ocean acidification is projected to greatly worsen in the foreseeable future. In conclusion, although ocean acidification did not contribute to the listing of *P. napopora* (79 FR 53851), the current information indicates that the species is likely to be susceptible to ocean acidification, that this threat has worsened since listing in 2014, and that it will greatly worsen in the foreseeable future (Table 17).

Disease: As noted in Section 3.2.3 above, since listing in 2014, the effects of disease on Indo-Pacific corals have increased, mainly in response to the 2014–2017 bleaching events. Generally, *Porites* species are susceptible to most of the diseases that infect coral, and are commonly affected by acute and lethal diseases (Brainard et al. 2014, 79 FR 53851, Aeby et al. 2016, Howells et al. 2020). Section 3.2.3 also describes how disease is projected to substantially worsen in the foreseeable future. In conclusion, the current information indicates that *P. napopora* continues to be susceptible to disease, that this threat has worsened since listing in 2014, and that it will substantially worsen in the foreseeable future (Table 17).

Fishing: As noted in Section 3.2.4 above, since listing in 2014, the direct and indirect effects of fishing on Indo-Pacific corals have continued, likely intensifying in some locations while lessening in others due to various factors. Generally, branching corals such as *P. napopora* may be more susceptible than other corals to damage by fishing gear because of their morphology (Brainard et al. 2011, 79 FR 53851). Section 3.2.4 also describes how fishing is projected to substantially worsen in the foreseeable future. In conclusion, the current information indicates that *P. napopora* continues to be susceptible to fishing, that this threat has continued since listing in 2014, and that it will substantially worsen in the foreseeable future (Table 17).

LBSP: As noted in Section 3.2.5 above, since listing in 2014, the effects of LBSP on Indo-Pacific corals have continued, likely intensifying in some locations while lessening in others due to various factors. Generally, *Porites* species have some susceptibility to turbidity and sediment (Brainard et al. 2011, 79 FR 53851, Carlson et al. 2019). Section 3.2.5 also describes how LBSP is projected to substantially worsen in the foreseeable future. In conclusion, the current information indicates that *P. napopora* continues to be susceptible to LBSP, that this threat has continued since listing in 2014, and that it will substantially worsen in the foreseeable future (Table 17).

Predation: As noted in Section 3.2.6 above, since listing in 2014, the effects of predation on Indo-Pacific corals have increased, mainly because the 2014–2017 bleaching events resulted in more favorable conditions for predators such as COTS. While the information available for the final listing indicated that *Porites* species generally have lower susceptibility to predation (Brainard et al. 2011, 79 FR 53851), recent studies show that *Porites* species can have higher susceptibility to predation especially when affected by warming-induced bleaching (Keesing et al. 2019, Tkachenko and Huang 2022). Section 3.2.6 also describes how predation is projected to substantially worsen in the foreseeable future. In conclusion, although predation did not contribute to the listing of *P. napopora* (79 FR 53851), the current information indicates that the species is likely to be susceptible to predation, that this threat has worsened since listing in 2014, and that it will greatly worsen in the foreseeable future (Table 17).

Collection and Trade: As noted in Section 3.2.7 above, since listing in 2014, the effects of collection and trade on Indo-Pacific corals have continued. According to the CITES database, since 2001, between 100,000 and over 300,000 *Porites* units were globally imported and exported annually. These units were not identified to species, thus may have included an undeterminable number of unidentified *P. napopora*. However, the database had no records of *P. napopora* (NMFS 2023a) and there is no other information to indicate that *P. diffluens* is particularly targeted for collection and trade. While Section 3.2.7 describes how collection and trade is projected to substantially worsen in the foreseeable future (Table 17), the current information does not indicate that collection and trade is a threat to *P. napopora*. Thus, we conclude that collection and trade has lower relative importance to the extinction risk of *P. napopora* (i.e., Low instead of Low-Medium) than for most of the other listed species.

Sea-level Rise: As noted in Section 3.2.8 above, since listing in 2014, sea-level rise has likely been too gradual to result in measurable effects on Indo-Pacific reef-building corals. In those cases where earthquakes have resulted in substrate uplift resembling sea-level rise, these substrates have been colonized by corals. In conclusion, as in the final rule, the current information indicates that *P. napopora* is not susceptible to sea-level rise, that there have been no detectable trends in the effects of this threat since listing in 2014, but that it will worsen in the foreseeable future (Table 17).

Regulatory Mechanisms: As noted in Section 3.2.9 above, since listing in 2014, some progress has been made with GHG management as well as controlling local threats although existing regulatory mechanisms are still inadequate to control any of the threats. Section 3.2.9 also describes how it is unlikely that regulatory mechanisms will be improved to the point where they are adequate to control any of the threats in the foreseeable future. In conclusion, the current information indicates that existing regulatory mechanisms remain inadequate to control any threat to *P. napopora*, and that improvement is unlikely in the foreseeable future (Table 17).

Threats Conclusion for *P. napopora*: Since *P. napopora* was listed in 2014, many of the threats to the species have worsened. All threats are projected to worsen in the foreseeable future, with the possible exception of regulatory mechanisms, which may continue to improve but also are likely to remain inadequate for controlling any of the threats (Table 17).

Although the final rule rated the relative importance of threats to the world's reef-building corals (Table 2), it did not apply those ratings to *P. napopora* (79 FR 53851). Instead, the final rule concluded that *P. napopora* is susceptible to ocean warming, disease, fishing, and LBSP, while regulatory mechanisms were inadequate for controlling any threat (79 FR 53851). However, as summarized above, we now have more genus-specific and species-specific information available on the importance of each of the threats to *Porites* species and *P. napopora*, respectively, which indicate that ocean acidification and predation are also likely to be impacting the status of the species. Based on the general importance ratings of the threats to Indo-Pacific reef-building corals (Table 3) and the genus-specific and species-specific information above, we conclude that the relative importance ratings of each threat to Indo-Pacific corals apply to *P. napopora*, with the exception of collection and trade (now rated as Low instead of Low-Medium). In addition, the observed threat trends since 2014 and projected threat trends in the foreseeable future are provided (Table 17).

Table 17. Summary of threats evaluation for *P. napopora*. For each threat, relative importance to the extinction risk of the species, observed trend since 2014, and projected trend in the foreseeable future are provided.

Threat (listing factor)	Importance	Observed Trend in Effects Since 2014	Projected Trend in Effects to 2100
Ocean Warming (Factor E)	Very High	Substantially worsened	Greatly worsen
Ocean Acidification (Factor E)	High	Worsened	Greatly worsen
Disease (Factor C)	High	Worsened	Substantially worsen
Fishing (Factor A)	Medium	Continued	Substantially worsen
LBSP (Factors A and E)	Low-Medium	Continued	Substantially worsen
Predation (Factor C)	Low-Medium	Worsened	Substantially worsen
Collection and Trade (Factor B)	Low	Continued	Substantially worsen
Sea-level Rise (Factor E)	Low	No detectable trends	Worsen
Inadequacy of Existing Regulatory Mechanisms (Factor D)	High	Some improvement but still inadequate	Improvement but likely still inadequate

4.14.5. Conclusion

As explained in the 2014 final listing rule (79 FR 53851), a species' vulnerability to extinction results from the combination of its spatial (i.e., distribution) and demographic (i.e., abundance) characteristics, threat susceptibilities, and consideration of the baseline environment and future projections of threats. *Porites napopora* was listed as threatened in 2014 because of its limited geographic distribution restricted largely to parts of the Coral Triangle and the western equatorial Pacific Ocean, susceptibilities to ocean warming, disease, fishing, and LBSP, inadequate regulatory mechanisms, declining baseline conditions, and projected worsening of threats (79 FR 53851).

Since 2014, we have learned that *P. napopora* has: (1) a broader depth distribution (3–17 m instead of 3–15 m); and (2) higher relative abundance (uncommon to common instead of rare to uncommon). That is, *P. napopora* is more broadly distributed and more abundant than we believed in 2014, and thus may have a higher capacity to moderate the effects of the threats, as explained in the Relevance of Distribution/Abundance to Status sections above.

Since 2014, the effects of ocean warming have substantially worsened, and the effects of most other threats have worsened as well. In addition, we have learned that *P. napopora* is also susceptible to ocean acidification and predation. All threats are projected to substantially worsen under current global GHG regulatory mechanisms, which would result in global warming of 2.6–3.4°C above the pre-industrial baseline by 2100 (see Fig. 4 in Section 3.1 above). Even if the goal of the Paris Agreement is achieved (i.e., limiting global warming to 1.5°C above pre-industrial by 2100), the threats would become much worse than they are currently (Dixon et al. 2022), likely preventing the recovery of *P. napopora*. Current regulatory mechanisms are grossly inadequate, especially GHG management.

In conclusion, the above information shows that *P. napopora* is more broadly distributed and more abundant than we believed in 2014, but that the threats have worsened and that ocean acidification and predation are also an important threat to the species. Especially concerning is that the most important threat to the species, ocean warming, has substantially worsened since the species was listed in 2014. The other important threats to the species, including ocean acidification, disease, fishing, LBSP, and predation have also either worsened or continued since 2014. While there has been some progress with regulatory mechanisms, primarily because of the 2016 Paris Agreement, regulatory mechanisms for both global and local threats are still inadequate. However, the species' distribution is broader and its abundance is greater than we were aware of at the time of listing in 2014, both of which are key factors for moderating threats.

4.15. *Seriatopora aculeata* (Quelch 1886)

4.15.1. Biology

Taxonomy. *Seriatopora aculeata* was described by Quelch (1886). It is included in the Corals of the World books (Veron 2000) and website (http://www.coralsoftheworld.org/, accessed August 2022), and is accepted by WoRMS (Hoeksma and Cairns 2021).

Morphology. Colonies are made up of pencil-diameter branches, which are usually short and always taper sharply at the end to a relatively sharp tip. The corallites on the sides of the branches, and irregularly spaced. Tentacles are commonly extended during the daytime. Colonies are yellow, pink or tan in color (Fig. 33, Fenner and Burdick 2016, Fenner 2020a, Veron et al. 2016).

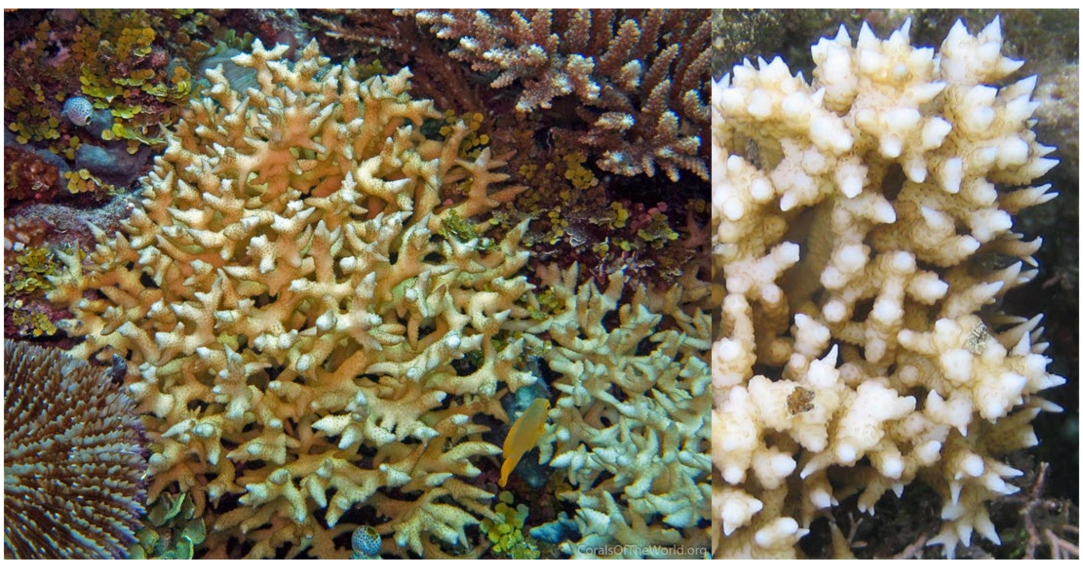


Figure 33. *Seriatopora aculeata*, showing colony (Emre Turak, Palau; Veron et al. 2016) and branch (Doug Fenner, Samoa) morphology.

Habitat. *Seriatopora aculeata* occurs in a broad range of habitats on the reef slope and back-reef, including but not limited to upper reef slopes, mid-slope terraces, lower reef slopes, reef flats, and lagoons (79 FR 53851). The Coral Traits Database (https://coraltraits.org/, accessed August 2022) lists *S. aculeata*'s water clarity preference as "clear," and wave exposure preference as "broad."

Life History. Little is known of the life history of *S. aculeata*, other *Seriatopora* species are hermaphroditic brooders. Larvae settle on suitable substrates such as rock or dead coral and grow into colonies (79 FR 53851).

4.15.2. Distribution

Geographic Distribution. *Seriatopora aculeata* has a relatively limited geographic distribution, occurring in 26 MEOWs (Fig. 34), based on information in NMFS (2022c). Its distribution is largely restricted to parts of the Coral Triangle region and the western equatorial Pacific Ocean. Despite the large number of islands and environments that are included in the species' range, it is mostly limited to an area projected to have the most rapid and severe impacts from climate change and localized human impacts for coral reefs over the 21st century. The current information indicates that *S. aculeata* occurs in four more MEOWs than we were aware of at the time of listing in 2014 (NMFS 2022c). These include MEOWs on the western (Chagos Islands) and eastern (Gilbert/Ellis Islands, Fiji, Tonga and Samoa) of its range, considerably expanding the geographic distribution of the species beyond what was known at the time of listing in 2014. Since we no longer consider the Mariana Islands MEOW to be within the range of the species (see U.S. Distribution below), but there are five new MEOWs, the total change since 2014 is an increase of four MEOWs.

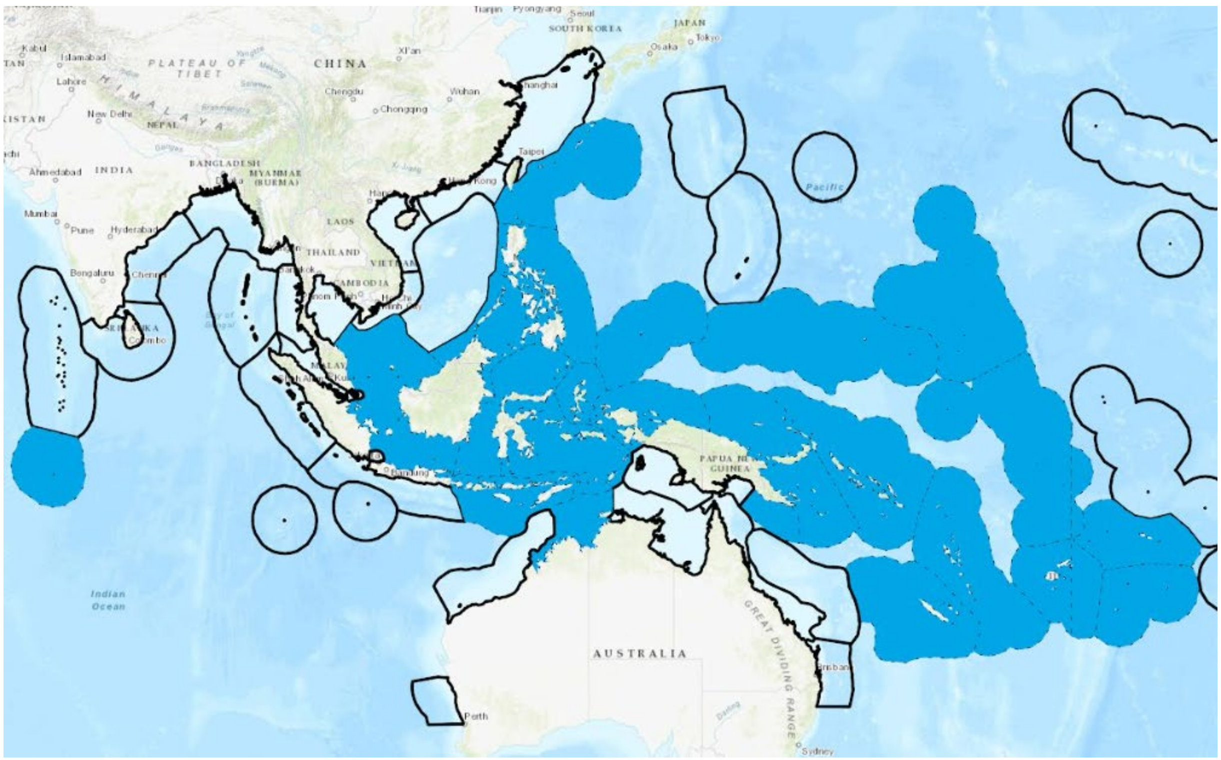


Figure 34. Geographic distribution of *S. aculeata*.

Depth Distribution. *Seriatopora aculeata* has a relatively broad depth distribution, occurring at depths of approximately 3–40 m (79 FR 53851, Coral Traits Database https://coraltraits.org/, accessed August 2022).

U.S. Distribution. *Seriatopora aculeata* was recorded in the Mariana Islands MEOW a handful of times between 1980 and 2010. However, despite a large number of expert surveys since then, it has not been recorded. Thus, the existing records do not support a conclusion that the Mariana Islands MEOW is within the current geographic distribution of the species (NMFS 2022c).

Relevance of Distribution to Status. Geographic and depth distributions were the key spatial factors considered in determining the status of coral species and in the listing of *S. aculeata* in 2014. A narrow geographic or depth distribution exacerbates a species' extinction risk because larger proportions of the population are likely to be exposed to any single disturbance. In contrast, a broad overall distribution moderates a species' extinction risk because the population is distributed across a range of geographic areas and depths, and thus lower proportions of the populations are likely to be exposed to any single disturbance (79 FR 53851). Since the geographic distribution of *S.*

aculeata is greater than we were aware of at the time of listing in 2014, its distribution has a greater capacity to moderate extinction risk.

4.15.3. Abundance

Relative Abundance. DeVantier and Turak (2017) characterized abundances of over 600 Indo-Pacific reef-building coral species in 31 Veron ecoregions from the Red Sea to Fiji, as further described in Section 4.1.3 above. *Seriatopora aculeata* was recorded in 17 of the 31 ecoregions. Within those 17 ecoregions, it had a mean overall abundance of 37.72 (Common), ranging from 1.94 (Uncommon) in the Sunda Shelf Ecoregion to 125.00 (Near Ubiquitous) in the Philippines North Ecoregion. The mean overall abundance of *S. aculeata* for all 31 ecoregions was 16.98 (Common, DeVantier and Turak 2017, Table S2), however some of the 14 ecoregions where it was not recorded may be outside its range. The Coral Traits Database (https://coraltraits.org/, accessed August 2022) lists *S. aculeata*'s global abundance estimate as "uncommon," but does not cite DeVantier and Turak (2017). Within its range, the relative abundance of *S. aculeata* may vary locally from very rare to at near ubiquitous. However, based on the above information, the rangewide relative abundance of *S. aculeata* is common. Thus, current information indicates that *S. aculeata* has a higher relative abundance (common) than we were aware of at the time of listing in 2014 (uncommon).

Absolute Abundance. Absolute abundance is an estimate of the total number of colonies of a species that currently exist throughout its range. Based on *S. aculeata'*s distribution and relative abundance, NMFS (2014) estimated the absolute abundance of *S. aculeata* to be at least millions of colonies. However, since then we have learned that the species has a broader geographic distribution and a higher relative abundance. Based on the updated information, *S. aculeata'*s absolute abundance is likely to be at least tens of millions of colonies. Thus, current information indicates that *S. aculeata* has a higher absolute abundance (at least tens of millions) than we were aware of at the time of listing in 2014 (at least millions).

Abundance Trends. As described above in the general Threats Evaluation and below for threats to *S. aculeata*, the most important threats (i.e., ocean warming, ocean acidification) have worsened since 2014, and substantial impacts to *Seriatopora* species have occurred, although no species-specific data are available for *S. aculeata*. Based on the continued worsening in the most important threats, it is likely that *S. aculeata* is decreasing in overall abundance (i.e., abundance across all the ecoregions that make up its range).

Relevance of Abundance to Status. Abundance is the key demographic factor considered in determining the status of coral species and in the listing of *S. aculeata* in 2014. A low relative or absolute abundance, especially in combination with declining abundance, exacerbates a species' extinction risk because larger proportions of the population are likely to be exposed to any single disturbance. In contrast, a higher relative or absolute abundance moderates a species' extinction risk because lower proportions of the population are likely to be exposed to any single disturbance (79 FR 53851). Since the relative abundance and absolute abundance of *S. aculeata* are both greater than we were aware of in at the time of listing in 2014, its abundance may have a greater capacity to moderate extinction risk.

4.15.4. Threats

This section provides an updated threats evaluation for *S. aculeata*, focusing on the threats that contributed to its listing (79 FR 53851), which included ocean warming, ocean acidification, disease, fishing, LBSP, collection and trade, and inadequacy of existing regulatory mechanisms. In addition, current information indicates that predation is also impacting the status of the species. A threats summary table is provided, including relative importance ratings for the threats, effects of threats since listing in 2014, and projected effects of threats in the foreseeable future.

Ocean Warming: As noted in Section 3.2.1 above, since listing in 2014, the effects of ocean warming on Indo-Pacific reef-building corals in general have substantially worsened. In response to the 2014–2017 series of warming-induced bleaching events, *Seriatopora* corals were among the most impacted coral taxa in different locations around the Indo-Pacific (e.g., Dalton et al. 2020, Frade et al 2018, Hughes et al. 2018a, Quimpo et al. 2020). Section 3.2.1 also describes how ocean warming is projected to greatly worsen in the foreseeable future (i.e., between now and 2100). In conclusion, the current information indicates that *S. aculeata* continues to be highly susceptible to ocean warming, that this threat has substantially worsened since listing in 2014, and that it will greatly worsen in the foreseeable future (Table 18).

Ocean Acidification: As noted in Section 2.2.2 above, since listing in 2014, the effects of ocean acidification on Indo-Pacific reef-building corals have worsened. Generally, *Seriatopora* species are susceptible to reduced calcification and skeletal growth from ocean acidification (Brainard et al. 2011, 79 FR 53851, Marcelino et al. 2017). Section 3.2.2 also describes how ocean acidification is projected to greatly worsen in the foreseeable future. In conclusion, the current information indicates that *S. aculeata* continues to be susceptible to ocean acidification, that this threat has worsened since listing in 2014, and that it will greatly worsen in the foreseeable future (Table 18).

Disease: As noted in Section 3.2.3 above, since listing in 2014, the effects of disease on Indo-Pacific corals have increased, mainly in response to the 2014–2017 bleaching events. Generally, *Seriatopora* species are susceptible to most of the diseases that infect coral, and are commonly affected by acute and lethal diseases (Brainard et al. 2011, 79 FR 53851, Ponti et al. 2016). Section 3.2.3 also describes how disease is projected to substantially worsen in the foreseeable future. In conclusion, the current information indicates that *S. aculeata* continues to be susceptible to disease, that this threat has worsened since listing in 2014, and that it will substantially worsen in the foreseeable future (Table 18).

Fishing: As noted in Section 3.2.4 above, since listing in 2014, the direct and indirect effects of fishing on Indo-Pacific corals have continued, likely intensifying in some locations while lessening in others due to various factors. Generally, branching corals such as *S. aculeata* may be more susceptible than other corals to damage by fishing gear because of their morphology (Brainard et al. 2011, 79 FR 53851). Section 3.2.4 also describes how fishing is projected to substantially worsen in the foreseeable future. In conclusion, the current information indicates that *S. aculeata* continues to be susceptible to fishing, that this threat has continued since listing in 2014, and that it will substantially worsen in the foreseeable future (Table 18).

LBSP: As noted in Section 3.2.5 above, since listing in 2014, the effects of LBSP on Indo-Pacific corals have continued, likely intensifying in some locations while lessening in others due to various factors. Generally, *Seriatopora* species are relatively susceptible to sediment and nutrients compared to other reef-building coral taxa (Brainard et al. 2011, 79 FR 53851, Carlson at al. 2019). Section 3.2.5 also describes how LBSP is projected to substantially worsen in the foreseeable future. In conclusion, the current information indicates that *S. aculeata* continues to be susceptible to LBSP, that this threat has continued since listing in 2014, and that it will substantially worsen in the foreseeable future (Table 18).

Predation: As noted in Section 3.2.6 above, since listing in 2014, the effects of predation on Indo-Pacific corals have increased, mainly because the 2014–2017 bleaching events resulted in more favorable conditions for predators such as COTS. While the information available for the final listing indicated lower susceptibility of *Seriatopora* species to predation (Brainard et al. 2011, 79 FR 53851), recent studies show that *Seriatopora* species can have higher susceptibility to predation by

COTS (Keesing 2021, Wilmes et al. 2020). Section 3.2.6 also describes how predation is projected to substantially worsen in the foreseeable future. In conclusion, although predation did not contribute to the listing of *S. aculeata* (79 FR 53851), the current information indicates that the species is likely susceptible to predation, that this threat has worsened since listing in 2014, and that it will greatly worsen in the foreseeable future (Table 18).

Collection and Trade: As noted in Section 3.2.7 above, since listing in 2014, the effects of collection and trade on Indo-Pacific corals have continued. According to the CITES database cited in Section 3.2.7, between 1985 and 2017, tens of thousands to hundreds of thousands of *Seriatopora* units were globally imported and exported annually. These units were not identified to species, thus may have included an undeterminable number of unidentified *S. aculeata*. The database recorded 5–10 *S. aculeata* units were globally imported and exported in 2008 and 2016, and none in any of the other years (NMFS 2022a). Because of the ongoing and projected growth in the industry, collection and trade may increasingly impact the status of *S. aculeata*. Section 3.2.7 also describes how collection and trade is projected to substantially worsen in the foreseeable future. In conclusion, the current information indicates that *S. aculeata* continues to be susceptible to collection and trade, that this threat has continued since listing in 2014, and that it will substantially worsen in the foreseeable future (Table 18).

Sea-level Rise: As noted in Section 3.2.8 above, since listing in 2014, sea-level rise has likely been too gradual to result in measurable effects on Indo-Pacific reef-building corals. In those cases where earthquakes have resulted in substrate uplift resembling sea-level rise, these substrates have been colonized by fast-growing corals such as *Seriatopora* species. In conclusion, as in the final rule, the current information indicates that *S. aculeata* is not susceptible to sea-level rise, that there have been no detectable trends in the effects of this threat since listing in 2014, but that it will worsen in the foreseeable future (Table 18).

Regulatory Mechanisms: As noted in Section 3.2.9 above, since listing in 2014, some progress has been made with GHG management as well as controlling local threats although existing regulatory mechanisms are still inadequate to control any of the threats. Section 3.2.9 also describes how it is unlikely that regulatory mechanisms will be improved to the point where they are adequate to control any of the threats in the foreseeable future. In conclusion, the current information indicates that existing regulatory mechanisms remain inadequate to control any threat to *S. aculeata*, and that improvement is unlikely in the foreseeable future (Table 18).

Threats Conclusion for *S. aculeata*: Since *S. aculeata* was listed in 2014, many of the threats to the species have worsened. All threats are projected to worsen in the foreseeable future, with the possible exception of regulatory mechanisms, which may continue to improve but also are likely to remain inadequate for controlling any of the threats (Table 18).

Although the final rule rated the relative importance of threats to the world's reef-building corals (Table 2), it did not apply those ratings to *S. aculeata* (79 FR 53851). Instead, the final rule concluded that *S. aculeata* is susceptible to ocean warming, disease, fishing, LBSP, and collection and trade while regulatory mechanisms were inadequate for controlling any threat (79 FR 53851). However, as summarized above, we now have more genus-specific and species-specific information available on the importance of each of the threats to *Seriatopora* species and *S. aculeata*, respectively, which indicate that predation is also likely to be impacting the status of the species. Based on the general importance ratings of the threats to Indo-Pacific reef-building corals (Table 3) and the genus-specific and species-specific information above, we conclude that the relative importance ratings of each threat to Indo-Pacific corals apply to *S. aculeata*. In addition, the observed threat trends since 2014 and projected threat trends in the foreseeable future are provided (Table 18).

Table 18. Summary of threats evaluation for *S. aculeata*. For each threat, relative importance to the extinction risk of the species, observed trend since 2014, and projected trend in the foreseeable future are provided.

Threat (listing factor)	Importance	Observed Trend in Effects Since 2014	Projected Trend in Effects to 2100
Ocean Warming (Factor E)	Very High	Substantially worsened	Greatly worsen
Ocean Acidification (Factor E)	High	Worsened	Greatly worsen
Disease (Factor C)	High	Worsened	Substantially worsen
Fishing (Factor A)	Medium	Continued	Substantially worsen
LBSP (Factors A and E)	Low-Medium	Continued	Substantially worsen
Predation (Factor C)	Low-Medium	Worsened	Substantially worsen
Collection and Trade (Factor B)	Low-Medium	Continued	Substantially worsen
Sea-level Rise (Factor E)	Low	No detectable trends	Worsen
Inadequacy of Existing Regulatory Mechanisms (Factor D)	High	Some improvement but still inadequate	Improvement but likely still inadequate

4.15.5. Conclusion

As explained in the 2014 final listing rule (79 FR 53851), a species' vulnerability to extinction results from the combination of its spatial (i.e., distribution) and demographic (i.e., abundance) characteristics, threat susceptibilities, and consideration of the baseline environment and future projections of threats. *Seriatopora aculeata* was listed as threatened in 2014 because of its limited geographic distribution largely restricted to parts of Coral Triangle region and western equatorial Pacific Ocean, high susceptibility to ocean warming, susceptibilities to ocean acidification, fishing, LBSP, disease, and collection and trade, inadequate regulatory mechanisms, declining baseline conditions, and projected worsening of threats (79 FR 53851).

Since 2014, we have learned that *S. aculeata* has a: (1) broader geographic distribution (26 MEOWs instead of 22); (2) higher relative abundance (common instead of uncommon); and (3) higher absolute abundance (at least tens of millions of colonies instead of at least millions of colonies) than we believed in 2014. That is, *S. aculeata* is more broadly distributed and more abundant than we believed in 2014, and thus may have a higher capacity to moderate the effects of the threats, as explained in the Relevance of Distribution/Abundance to Status sections above.

Since 2014, the effects of ocean warming have substantially worsened, and the effects of most other threats have worsened as well. All threats are projected to substantially worsen under current global GHG regulatory mechanisms, which would result in global warming of 2.6–3.4°C above the pre-industrial baseline by 2100 (see Fig. 4 in Section 3.1 above). Even if the goal of the Paris Agreement is achieved (i.e., limiting global warming to 1.5°C above pre-industrial by 2100), the threats would become much worse than they are currently (Dixon et al. 2022), likely preventing the recovery of *S. aculeata*. Current regulatory mechanisms are grossly inadequate, especially GHG management.

In conclusion, the above information shows that *S. aculeata* is more broadly distributed and more abundant than we believed in 2014, but that the threats have worsened and that predation is also an important threat to the species. Especially concerning is that the most important threat to the species, ocean warming, has substantially worsened since the species was listed in 2014. The other important threats to the species, including ocean acidification, disease, fishing, LBSP, predation, and collection and trade have also either worsened or continued since 2014. While there has been some progress with regulatory mechanisms, primarily because of the 2016 Paris Agreement, regulatory mechanisms for both global and local threats are still inadequate. However, the species' distribution is broader and its abundance is greater than we were aware of at the time of listing in 2014, both of which are key factors for moderating threats.

5. Literature Cited

Adam TC, Burkepile DE, Holbrook SJ, et al. 2021. Landscape-scale patterns of nutrient enrichment in a coral reef ecosystem: implications for coral to algae phase shifts. Ecological Applications 31(1). https://doi.org/10.1002/eap.2227

Adams J. 2014. Introducing the Red Devil *Acropora tenella* from Kwajalein Atoll. https://reefbuilders.com/2014/03/28/red-devil-acropora-tenella-kwajalein-atoll/

Adams J. 2015. Shallow water *Acropora globiceps* looks like living crystals. https://reefbuilders.com/2015/07/03/acropora-globiceps/

Adams J. 2016. Pink *Acropora jacquelineae* discovered in Raja Ampat. https://reefbuilders.com/2016/01/27/acropora-jacquelineae/

Adams J. 2018. Top 5 Super Exotic Thin Branched Acroporas. https://reefbuilders.com/2018/11/07/top-5-super-exotic-thin-branched-acroporas/

Adams J. 2019. Five Super Exotic Thick Branching Acropora Species. https://reefbuilders.com/2019/03/12/five-super-exotic-acropora-species/

Adams J. 2022. World's First Grafted Anacropora Pops up for Reef Raft. https://reefbuilders.com/2022/03/01/worlds-first-grafted-anacropora-pops-up-for-reef-raft/

Adjeroud M, Mauguit Q, Penin L. 2015. The size-structure of corals with contrasting life-histories: A multiscale analysis across environmental conditions. Marine Environmental Research 112:131-139.

Adyasari D, Pratama MA, Teguh NA, et al. 2021. Anthropogenic impact on Indonesian coastal water and ecosystems: Current status and future opportunities. Marine Pollution Bulletin 171: 112689, ISSN 0025-326X, https://doi.org/10.1016/j.marpolbul.2021.112689.

Aeby GS, Callahan S, Cox EF, et al. 2016. Emerging coral diseases in Kāne'ohe Bay, O'ahu, Hawai'i (USA): two major disease outbreaks of acute Montipora white syndrome. Dis Aquat Organ 119(3):189-98. https://doi.org/10.3354/dao02996

Aeby GS, Howells E, Work T., et al. 2020. Localized outbreaks of coral disease on Arabian reefs are linked to extreme temperatures and environmental stressors. Coral Reefs 39, 829–846. https://doi.org/10.1007/s00338-020-01928-4

Agostini S, Harvey BP, Wada S, et al. 2018. Ocean acidification drives community shifts towards simplified non-calcified habitats in a subtropical-temperate transition zone. Sci Rep. 8(1):11354. https://doi.org/10.1038/s41598-018-29251-7

AIMS (Australian Institute of Marine Science). 2022. Long-term reef monitoring program annual summary report on coral reef condition 2021/22. https://www.aims.gov.au/monitoring-great-barrier-reef/gbr-condition-summary-2021-22

Albert S, Saunders MI, Roelfsema CM, et al. 2017. Winners and losers as mangrove, coral and seagrass ecosystems respond to sea-level rise in the Solomon Islands. Environmental Research Letters. 12(9). https://doi.org/10.1088/1748-9326/aa7e68

Albright R, Takeshita Y, Koweek DA, et al. 2018. Carbon dioxide addition to coral reef waters suppresses net community calcification. Nature. 555(7697):516-519. https://doi.org/10.1038/nature25968

Allgeier JE, Andskog MA, Hensel E, et al. 2020. Rewiring coral: Anthropogenic nutrients shift diverse coral–symbiont nutrient and carbon interactions toward symbiotic algal dominance. Glob Change Biol. 26: 5588– 5601. https://doi.org/10.1111/gcb.15230

Anderson KD, Cantin NE, Casey JM, et al. 2019. Independent effects of ocean warming versus acidification on the growth, survivorship and physiology of two Acropora corals. Coral Reefs 38, 1225–1240 (2019). https://doi.org/10.1007/s00338-019-01864-y

Anthony KRN. 2016. Coral reefs under climate change and ocean acidification: Challenges and opportunities for management and policy. Annual Review of Environment and Resources. 41(1):59-81.

Ateweberhan M, McClanahan TR, Graham NAJ, Sheppard CRC. 2011. Episodic heterogeneous decline and recovery of coral cover in the indian ocean. Coral Reefs. 30:739-752.

Aurellado MEB, Ticzon VS, Nañola CL, et al. 2021. Effectiveness of Philippine Nationally Managed Marine Reserves in Improving Biomass and Trophic Structure of Coral Reef Fish Communities. Coastal Management, 49:293-312. https://doi.org/10.1080/08920753.2021.1899944

Baird, A.H., Guest, J.R. and Willis, B.L., 2009. Systematic and biogeographical patterns in the reproductive biology of scleractinian corals. Annual Review of Ecology, Evolution, and Systematics, 40, pp.551-571.

Bairos-Novak KR, Hoogenboom MO, van Oppen MJH, et al. 2021. Coral adaptation to climate change: Meta-analysis reveals high heritability across multiple traits. Glob Chang Biol. (22):5694-5710. doi: 10.1111/gcb.15829

Baker AC, Glynn PW, Riegl B. 2008. Climate change and coral reef bleaching: An ecological assessment of long-term impacts, recovery trends and future outlook. Estuar Coast Shelf S. 80(4):435-471

Ballesteros LV, Matthews JL, Hoeksema BW. 2018. Pollution and coral damage caused by derelict fishing gear on coral reefs around Koh Tao, Gulf of Thailand.Marine Pollution Bulletin 135:1107-1116. https://doi.org/10.1016/j.marpolbul.2018.08.033.

Barkley HC, Cohen AL, Golbuu Y, et al. 2015. Changes in coral reef communities across a natural gradient in seawater pH. Marine Ecology. 2015;1:e1500328.

Baumann JH, Zhao LZ, Stier A.C, et al. 2022. Remoteness does not enhance coral reef resilience. Global Change Biology, 28, 417– 428. https://doi.org/10.1111/gcb.15904

Becker M, Meyssignac B, Letetrel C, et al. 2012. Sea-level variations at tropical Pacific islands since 1950. Global and Planetary Change. 80-81:85-98.

Ben-Zvi, O, Eyal G, Loya Y. 2019. Response of fluorescence morphs of the mesophotic coral *Euphyllia paradivisa* to ultra-violet radiation. Sci Rep 9, 5245. https://doi.org/10.1038/s41598-019-41710-3

Ben-Zvi, O, Tamir R, Keren N. et al. 2020. Photophysiology of a mesophotic coral 3 years after transplantation to a shallow environment. Coral Reefs 39, 903–913. https://doi.org/10.1007/s00338-020-01910-0

Bernard, HM. 1897. Catalogue of the Madreporarian Corals in the British Museum (Natural History). Volume III. The Genus Montipora. The Genus Anacropora. 274 p.

Berumen ML, Pratchett MS. 2006. Recovery without resilience: Persistent disturbance and long-term shifts in the structure of fish and coral communities at tiahura reef, moorea. Coral Reefs. 25(4):647-653.

Bessey C, Babcock RC, Thomson DP, et al. 2018. Outbreak densities of the coral predator Drupella in relation to in situ Acropora growth rates on Ningaloo Reef, Western Australia. Coral Reefs 37, 985–993. https://doi.org/10.1007/s00338-018-01748-7

Birkeland C. 2019. Global status of coral reefs: In combination, disturbances and stressors become ratchets. World Seas: An Environmental Evaluation, p. 35-56. https://doi.org/10.1016/B978-0-12-805052-1.00002-4

Blake, B. 2022. Coral Profile: The Frogspawn Corals. https://www.boodleshireaquatics.com/post/coral-profile-the-frogspawn-corals

Bourne DG, Ainsworth TD, Pollock FJ, et al. 2015. Towards a better understanding of white syndromes and their causes on Indo-Pacific coral reefs. Coral Reefs 34, 233–242. https://doi.org/10.1007/s00338-014-1239-x

Bowden-Kerby A, Kirata T, Romeo L. 2021. Restoration and Natural Recovery of Corals after Unprecedented Mass Bleaching and Coral Death in the Line Islands, Kiribati. Working Paper, of work completed June 2016 through March 2020. Corals for Conservation https://corals4conservation.org/

Brainard RE, Birkeland C, Eakin CM, et al. 2011. Status review report of 82 candidate coral species petitioned under the U.S. Endangered Species Act. Pacific Islands Fisheries Science Center, Honolulu, HI.

Brainard RE, Asher J, Blyth-Skyrme V, et al. 2012. Coral reef ecosystem monitoring report of the Mariana Archipelago: 2003-2007. Pacific Islands Fisheries Science Center, PIFSC Special Publication SP-12-01.

Bramante JF, Ashton AD, Storlazzi CD, et al. 2020. Sea level rise will drive divergent sediment transport patterns on fore reefs and reef flats, potentially causing erosion on atoll islands. Journal of Geophysical Research: Earth Surface, 125, e2019JF005446. https://doi.org/10.1029/2019JF005446

Bridge TCL, Webster JM, Sih TL, et al. 2019. The GBR outer-shelf. In: Hutchings P.A., M. Kingsford, and O. Hoegh-Guldberg (eds), The GBR: Biology, Environment and Management, p. 73-84. EBSCO Publishing.

Brodnicke OB, Bourne DG, Heron SF et al. 2019. Unravelling the links between heat stress, bleaching and disease: fate of tabular corals following a combined disease and bleaching event. Coral Reefs 38, 591–603. https://doi.org/10.1007/s00338-019-01813-9

Brook G. 1892. Preliminary descriptions of new species of Madrepora in the collections of the British Museum. Part II. Annals and Magazine of Natural History 10:451-465.

Browne N, Braoun C, McIlwain J, Nagarajan R, Zinke J. 2019. Borneo coral reefs subject to high sediment loads show evidence of resilience to various environmental stressors. PeerJ. 2019 7:e7382. https://doi.org/10.7717%2Fpeerj.7382

Bruckner AW, Coward G, Bimson K. et al. 2017. Predation by feeding aggregations of Drupella spp. inhibits the recovery of reefs damaged by a mass bleaching event. Coral Reefs 36, 1181–1187. https://doi.org/10.1007/s00338-017-1609-2

Bruno JF, Selig ER. 2007. Regional decline of coral cover in the indo-pacific: Timing, extent, and subregional comparisons. PLoS one. 2(8):e711.

Bruno JF, Cote IM, Toth LT. 2019. Climate change, coral loss, and the curious case of the parrotfish paradigm: Why don't marine protected areas improve reef resilience? Ann Rev Mar Sci. 11:307-334. https://doi.org/10.1146/annurev-marine-010318-095300

Burke L, Reytar K, Spalding M, Perry A. 2011. Reefs at Risk Revisited. World Resources Institute.

Burke, S., Pottier, P., Lagisz, M., Macartney, E.L., Ainsworth, T., Drobniak, S.M. et al. 2023. The impact of rising temperatures on the prevalence of coral diseases and its predictability: A global meta-analysis. Ecology Letters, 00, 1–16. Available from: https://doi.org/10.1111/ele.14266

Burkepile DE, Shantz AA, Adam TC, et al. 2020. Nitrogen Identity Drives Differential Impacts of Nutrients on Coral Bleaching and Mortality. Ecosystems 23, 798–811. https://doi.org/10.1007/s10021-019-00433-2

Burt JA, Camp EF, Enochs IC, et al. 2020. Insights from extreme coral reefs in a changing world. Coral Reefs 39, 495–507. https://doi.org/10.1007/s00338-020-01966-y

Camp EF, Nitschke MR, Rodolfo-Metalpa R, et al. 2017. Reef-building corals thrive within hot-acidified and deoxygenated waters. Sci Rep 7, 2434. https://doi.org/10.1038/s41598-017-02383-y

Campbell SJ, Darling ES, Pardede S, et al. 2020. Fishing restrictions and remoteness deliver conservation outcomes for Indonesia's coral reef fisheries. Conservation Letters https://doi.org/10.1111/conl.12698

Cannon SE, Aram E, Beiateuea T, et al. 2021. Coral reefs in the Gilbert Islands of Kiribati: Resistance, resilience, and recovery after more than a decade of multiple stressors. PLoS ONE 16(8): e0255304. https://doi.org/10.1371/journal.pone.0255304

Carlson RR, Foo SA and Asner GP. 2019. Land Use Impacts on Coral Reef Health: A Ridge-to-Reef Perspective. Front. Mar. Sci. 6:562. https://doi.org/10.3389/fmars.2019.00562

Carpenter KE, Abrar M, Aeby G, et al. 2008. One-third of reef-building corals face elevated extinction risk from climate change and local impacts. Science 321(5888):560-563.

CBD (Center for Biological Diversity). 2009. Petition to list 83 coral species under the Endangered Species Act. Submitted October 20th, 2009, to the U.S. Secretary of Commerce.

CBD (Center for Biological Diversity). 2018. Petition to list the caulifower coral *Pocillopora meandrina* in Hawaii as endangered or threatened under the Eangered Species Act. Submitted March 14th, 2018, to the U.S. Secretary of Commerce.

CBD (Center for Biological Diversity). 2020. Petition for Protective Regulations Under Section 4(d) of the Endangered Species Act for the Conservation of Threatened Corals. Submitted February 20, 2020, to the U.S. Secretary of Commerce.

CBD (Center for Biological Diversity). 2021. Public comment on NOAA-NMFS-2020-0151, Endangered and Threatened Species; Notice of Initiation of 5- Year Review of Indo-Pacific Reef-building Coral, 86 Fed. Reg. 1090 (Jan. 7, 2021). Submitted via email to Lance Smith, on February 8, 2021.

Chalias, V. 2019a. *Acropora lokani* is SPS Royalty Among Acros. https://reefbuilders.com/2019/11/25/acropora-lokani/

Chalias, V. 2019b. *Acropora lokani*: The great Indonesian classic. https://recifalnews.fr/2019/07/acropora-lokani-le-grand-classique-indonesien/

Chalias, V. 2019c. Flaming Sunrise from Candy Corals is one of a Helluva *Acropora speciosa*. https://reefbuilders.com/2019/05/20/flaming-sunrise-from-candy-corals-is-one-of-a-helluva-acropora-speciosa/

Cheal AJ, MacNeil MA, Cripps E, et al. 2010. Coral–macroalgal phase shifts or reef resilience: Links with diversity and functional roles of herbivorous fishes on the great barrier reef. Coral Reefs. 29:1005-1015.

Chen T, Roff G, McCook L, et al. 2018. Recolonization of marginal coral reef flats in response to recent sea-level rise. Journal of Geophysical Research: Oceans, 123, 7618–7628. https://doi.org/10.1029/2018JC014534

Cheung MWM, Hock K, Skirving W, et al. 2021. Cumulative bleaching undermines systemic resilience of the Great Barrier Reef. Current Biology 31:5385-5392. https://doi.org/10.1016/j.cub.2021.09.078

Cinner JE, Zamborain-Mason J, Gurney GG, et al. 2020. Meeting fisheries, ecosystem function, and biodiversity goals in a human-dominated world. Science 368, Issue 6488, pp. 307-311. https://www.science.org/doi/10.1126/science.aax9412

Colin PL, Lindfield SJ. 2019. Palau. In: Loya Y., Puglise K., Bridge T. (eds), Mesophotic Coral Ecosystems, p. 285 - 289. Springer.

Commonwealth Blue Charter. 2021. Case Study, Marine Protected Areas. Seychelles - Using Marine Spatial Planning to Meet the 30 Per Cent Marine Protected Area Target.

Connell JH. 1997. Disturbances and recovery of coral assemblages. Coral Reefs. 16(Supplement):S101-S113.

Connell JH, Hughes TP, Wallace CC. 1997. A 30-year study of coral abundance, recruitment, and disturbance at several scales in space and time. Ecological Monographs. 67(4):461-488.

Cornwall CE, Comeau S, Kornder NA, et al. 2021. Global declines in coral reef calcium carbonate production under ocean acidification and warming. PNAS 118 (21) e2015265118. https://doi.org/10.1073/pnas.2015265118

Cosain-Díaz JA, Tortolero-Langarica JJA, Rodríguez-Troncoso AP, et al. 2021. Internal bioerosion in massive corals associated with reef communities in the northeastern tropical Pacific: The effect of intrinsic and extrinsic factors. Ciencias Marinas 47(1):33–47. https://doi.org/10.7773/cm.v47i1.3047

Couch CS, Burns JHR, Liu G, et al. 2017. Mass coral bleaching due to unprecedented marine heatwave in Papahanaumokuakea Marine National Monument (Northwestern Hawaiian Islands). PLoS One. 12(9):1-27. https://doi.org/10.1371/journal.pone.0185121

Crompton O, Corrêa D, Duncan J, et al. 2021. Deforestation-induced surface warming is influenced by the fragmentation and spatial extent of forest loss in Maritime Southeast Asia. Environmental Research Letters, Volume 16, Number 11: https://iopscience.iop.org/article/10.1088/1748-9326/ac2fdc

Dalton SJ, Carroll AG, Sampayo E, et al. 2020. Successive marine heatwaves cause disproportionate coral bleaching during a fast phase transition from El Niño to La Niña. Sci Total Environ 715:136951. https://pubmed.ncbi.nlm.nih.gov/32014776/

Dana JE. 1846. Zoophytes. United States Exploring Expedition 1838-1842 7: 740 pp.

Darling ES, Alvarez-Filip L, Oliver TA, et al. 2012. Evaluating life-history strategies of reef corals from species traits. Ecology Letters 15:1378-1386.

Das RR, Wada H, Masucci GD, et al. 2022. Four-Year Field Survey of Black Band Disease and Skeletal Growth Anomalies in Encrusting *Montipora* spp. Corals around Sesoko Island, Okinawa. Diversity 14, 32. https://doi.org/10.3390/d14010032

Davis KL, Colefax AP, Tucker JP. et al. 2021. Global coral reef ecosystems exhibit declining calcification and increasing primary productivity. Commun Earth Environ 2, 105. https://doi.org/10.1038/s43247-021-00168-w

De'ath G, Fabricius KE, Sweatman H, et al. 2012. The 27-year decline of coral cover on the great barrier reef and its causes. Proceedings of the National Academy of Sciences of the United States of America. 109(44):17995-17999.

Denis V, Soto D, De Palmas S, et al. 2019. Taiwan. In: Loya Y., Puglise K., Bridge T. (eds) Mesophotic Coral Ecosystems, p. 249 - 264. Springer.

DeVantier L, Turak E. 2017. Species richness and relative abundance of reef-building corals in the Indo-west Pacific. Diversity. 9(3):1-30. https://doi.org/10.3390/d9030025

Dietzel A, Bode M, Connolly SR, et al. 2020. Long-term shifts in the colony size structure of coral populations along the Great Barrier Reef. Proc. R. Soc. B 287: 20201432. http://dx.doi.org/10.1098/rspb.2020.1432

Dietzel A, Bode M, Connolly SR, et al. 2021. The population sizes and global extinction risk of reef-building coral species at biogeographic scales. Nature Ecology & Evolution. https://doi.org/10.1038/s41559-021-01393-4

Dietzel A, Bode M, Connolly SR, et al. 2022. Reply to: Conclusions of low extinction risk for most species of reef-building corals are premature. Nature Ecology & Evolution https://doi.org/10.1038/s41559-022-01659-5

Dixon AM, Forster PM, Heron SF, et al. 2022. Future loss of local-scale thermal refugia in coral reef ecosystems. PLOS Clim 1(2): e0000004. https://doi.org/10.1371/journal.pclm.0000004

Donovan MK, Adam TC, Shantz AA, et al. 2020. Nitrogen pollution interacts with heat stress to increase coral bleaching across the seascape. Proc Natl Acad Sci USA. 117(10):5351-5357. https://doi.org/10.1073/pnas.1915395117

Donovan MK, Burkepile DE, Kratochwill C, et al. 2021. Local conditions magnify coral loss after marine heatwaves. Science https://www.science.org/doi/10.1126/science.abd9464

Dunning HK. 2014. Ecosystem services and community based coral reef management institutions in post blast-fishing Indonesia. Ecosystem Services. http://dx.doi.org/10.1016/j.ecoser.2014.11.010i

Dustan P, Doherty O, Pardede S. 2013. Digital reef rugosity estimates coral reef habitat complexity. PloS one. 8(2):e57386.

Eakin CM, Liu G, Gomez AM, et al. 2017. Ding, dong, the witch is dead (?) - 3 years of global coral bleaching 2014-2017. Reef Currents Reef Encounter The News Journal of the International Society for Reef Studies. 32(1):33-38.

Eakin CM, Sweatman HPA, Brainard RE. 2019. The 2014–2017 global-scale coral bleaching event: insights and impacts. Coral Reefs 38:539–545. https://doi.org/10.1007/s00338-019-01844-2

Elder H, Weis VM, Montalvo-Proano J, et al. 2022. Genetic Variation in Heat Tolerance of the Coral *Platygyra daedalea* Indicates Potential for Adaptation to Ocean Warming. Front. Mar. Sci. 9:925845. https://doi.org/10.3389/fmars.2022.925845

Ellis JI, Jamil T, Anlauf H, et al. 2019. Multiple stressor effects on coral reef ecosystems. Global Change Biology 25:4131–4146. https://doi.org/10.1111/gcb.14819

Evensen NR, Bozec Y-M, Edmunds PJ, et al. 2021. Scaling the effects of ocean acidification on coral growth and coral–coral competition on coral community recovery. PeerJ 9:e11608 https://doi.org/10.7717/peerj.11608

Eyal G, Eyal-Shaham L, Cohen R, et al. 2016. *Euphyllia paradivisa*, a successful mesophotic coral in the northern Gulf of Eilat/Aqaba, Red Sea. Coral Reefs 35: 91-102. https://doi.org/10.1007/s00338-015-1372-1

Eyal G, Tamir R, Kramer N. et al. 2019. The Red Sea: Israel. Pp 199-214 in Loya, Y., Puglise, K. A., Bridge, T. C. E. (Eds.) Mesophotic Coral Ecosystems. Springer.

Eyre BD, Cyronak T, Drupp P, et al. 2018. Coral reefs will transition to net dissolving before end of century. Science. 359(6378):908-911. https://www.science.org/doi/10.1126/science.aao1118

Fabricius KE, Noonan SHC, Abrego D, et al. 2017. Low recruitment due to altered settlement substrata as primary constraint for coral communities under ocean acidification. Proc. R. Soc. B 284: 20171536. http://dx.doi.org/10.1098/rspb.2017.1536

Feely RA, Doney SC, Cooley SR. 2009. Ocean acidification: Present conditions and future changes in a high CO_2 world. Oceanography: Special Issue feature. 22, No. 4.

Feely RA, Doney SC, Cooley SR. 2012. Present conditions and future conditions in a high-CO_2 world. Oceanography. 22(4):36-47.

Fenner, D. 2001. Reef corals of the Togean and Banggai Islands, Sulawesi, Indonesia. Pp 18-26 in Allen, G.R., and S.A. McKenna (Eds.) A Marine Rapid Assessment of the Togean and Banggai Islands, Sulawesi, Indonesia. RAP Bulletin of Biological Assessment 20, Conservation International, Washington, DC.

Fenner 2020a. Field Guide to the Coral Species of the Samoan Archipelago: American Samoa and The Independent State of Samoa. Version 2.5. 582 p. Available from douglasfennertassi@gmail.com

Fenner, D. 2020b. Unpublished data on the distribution and abundance of ESA-listed corals in the U.S. Pacific Islands and neighboring countries.

Fenner, D, Burdick D. 2016. Field Identification Guide to the Threatened Corals of the U.S. Pacific Islands. 80 p. https://www.coris.noaa.gov/activities/Corals_FieldID/

Figueroa-Pico J, Tortosa FS, Carpio AJ. 2020. Coral fracture by derelict fishing gear affects the sustainability of the marginal reefs of Ecuador. Coral Reefs 39, 819–827. https://doi.org/10.1007/s00338-020-01926-6

Fox, MD, Carter AL, Edwards CB et al. 2019. Limited coral mortality following acute thermal stress and widespread bleaching on Palmyra Atoll, central Pacific. Coral Reefs 38, 701–712. https://doi.org/10.1007/s00338-019-01796-7

Fox MD, Cohen AL, Rotjan RD, et al. 2021. Increasing coral reef resilience through successive marine heatwaves. Geophysical Research Letters, 48, e2021GL094128. https://doi.org/10.1029/2021GL094128

Frade PR, Bongaerts P, Englebert N. et al. 2018. Deep reefs of the Great Barrier Reef offer limited thermal refuge during mass coral bleaching. Nat Commun 9, 3447. https://doi.org/10.1038/s41467-018-05741-0

Fujii T, Kitano YF, Tachikawa H. 2020. New Distributional Records of Three Species of Euphylliidae (Cnidaria, Anthozoa, Hexacorallia, Scleractinia) from the Ryukyu Islands, Japan, Species Diversity 25: 275-282. https://doi.org/10.12782/specdiv.25.275

Gardiner JS. 1898. On the perforate corals collected by the author in the South Pacific. Proceedings of the Zoological Society of London 66: 257-276.

GCRMN (Global Coral Reef Monitoring Network). 2020. Status of Coral Reefs of the World: 2020. Edited by: David Souter, Serge Planes, Jérémy Wicquart, Murray Logan, David Obura and Francis Staub. International Coral Reef Initiative https://gcrmn.net/2020-report/

Gilmour JP, Cook KL, Ryan NM, et al. 2022. A Tale of Two Reef Systems: Local Conditions, Disturbances, Coral Life Histories, and the Climate Catastrophe. Ecological Applications 32(3): e2509. https://doi.org/10.1002/eap.2509

Glynn PW. 2001. Eastern Pacific Coral Reef Ecosystems. Pp. 281-305 in: Seeliger, U. and Kjerfve, B. (eds.). Ecological Studies Vol. 144, Coastal Marine Ecosystems of Latin America, Springer-Verlag Berlin Heidelberg.

Godefroid M, Arçuby R, Lacube Y, et al. 2021. More than local adaptation: high diversity of response to seawater acidification in seven coral species from the same assemblage in French Polynesia. Journal of the Marine Biological Association of the United Kingdom 101, 675–683. https://doi.org/10.1017/S0025315421000618

Gomez, ED, Alcala AC, San Diego AC. 1981. Status of Philippine coral reefs – 1981. Proceedings of the Fourth International Coral Reef Symposium, Manila, 1981. 1:275-282.

Graham NAJ, Bellwood DR, Cinner JE, et al. 2013. Managing resilience to reverse phase shifts in coral reefs. Frontiers in Ecology and the Environment. 11(10):541-548.

Graham NAJ, McClanahan TR, MacNeil MA, et al. 2017. Human Disruption of Coral Reef Trophic Structure. Current Biology 27:231–236. https://doi.org/10.1016/j.cub.2016.10.062

Grand View Research. 2022. Reef Aquarium Market Size, Share & Trends Analysis. Report Overview. https://www.grandviewresearch.com/industry-analysis/reef-aquarium-market-report

Greene A, Donahue MJ, Caldwell JM, et al. 2020. Coral Disease Time Series Highlight Size-Dependent Risk and Other Drivers of White Syndrome in a Multi-Species Model. Front. Mar. Sci. 7:601469. https://doi.org/10.3389/fmars.2020.601469

Guan Y, Hohn S, Wild C, et al. 2020. Vulnerability of global coral reef habitat suitability to ocean warming, acidification, and eutrophication. Global Change Biology 26:5646–5660. https://doi.org/10.1111/gcb.15293

Guest JR, Edmunds PJ, Gates RD, et al. 2018. A framework for identifying and characterising coral reef "oases" against a backdrop of degradation. Journal of Applied Ecology. 55(6):2865-2875 https://doi.org/10.1111/1365-2664.13179

Guillermic M, Cameron LP, De Corte I, et al. 2021. Thermal stress reduces pocilloporid coral resilience to ocean acidification by impairing control over calcifying fluid chemistry. Sci Adv https://www.science.org/doi/10.1126/sciadv.aba9958

Guo W, Bokade R, Cohen AL, et al. 2020. Ocean acidification has impacted coral growth on the Great Barrier Reef. Geophysical Research Letters, 47, e2019GL086761. https://doi.org/10.1029/2019GL086761

Hadaidi G, Ziegler M, Shore-Maggio A, et al. 2018. Ecological and molecular characterization of a coral black band disease outbreak in the Red Sea during a bleaching event. PeerJ. 6:e5169. https://doi.org/10.7717/peerj.5169

HadCRUT (Hadley Centre and the University of East Anglia's Climatic Research Unit). 2022. HadCRUT's global temperature dataset, https://crudata.uea.ac.uk/cru/data/temperature/

Harriott VJ. 1992. Recruitment patterns of scleractinian corals in an isolated sub-tropical reef system. Coral Reefs 11, 215–219.

Haywood MDE, Thomson DP, Babcock RC. et al. 2019. Crown-of-thorns starfish impede the recovery potential of coral reefs following bleaching. Mar Biol 166:99. https://doi.org/10.1007/s00227-019-3543-z

Heenan A, Williams GJ, Williams ID. 2019. Natural variation in coral reef trophic structure across environmental gradients. Front Ecol Environ 18(2): 69–75. https://doi.org/10.1002/fee.2144

Heron SF, Maynard JA, van Hooidonk R, et al. 2016. Warming trends and bleaching stress of the world's coral reefs 1985-2012. Sci Rep. 6:38402. https://doi.org/10.1038/srep38402

Heron SF, Eakin CM, Douvere F, et al. 2017. Impacts of climate change on world heritage coral reefs: A first global scientific assessment. UNESCO World Heritage Centre.

Hill TS, Hoogenboom MO. 2022. The indirect effects of ocean acidification on corals and coral communities. Coral Reefs https://doi.org/10.1007/s00338-022-02286-z

Hobbs J-PA, Frisch AJ, Newman SJ, et al. 2015. Selective Impact of Disease on Coral Communities: Outbreak of White Syndrome Causes Significant Total Mortality of Acropora Plate Corals. PLoS ONE 10(7): e0132528. https://doi.org/10.1371/journal.pone.0132528

Hock K, Wolff NH, Ortiz JC, et al. 2017. Connectivity and systemic resilience of the Great Barrier Reef. PLoS Biol. 15(11):e2003355. https://doi.org/10.1371/journal.pbio.2003355

Hoegh-Guldberg O, Poloczanska ES, Skirving W, et al. 2017. Coral reef ecosystems under climate change and ocean acidification. Frontiers in Marine Science. 4:1-20. https://doi.org/10.3389/fmars.2017.00158

Hoeksma BW, Cairns S. 2021. World Register of Marine Species. https://www.marinespecies.org/index.php, accessed Mar 2022.

Hoogenboom MO, Frank GE, Chase TJ, et al. 2017. Environmental Drivers of Variation in Bleaching Severity of Acropora Species during an Extreme Thermal Anomaly. Front. Mar. Sci. 4:376. https://doi.org/10.3389/fmars.2017.00376

Howells EJ, Vaughan GO, Work TM. et al. 2020. Annual outbreaks of coral disease coincide with extreme seasonal warming. Coral Reefs 39, 771–781. https://doi.org/10.1007/s00338-020-01946-2

Hughes TP, Connell JH. 1999. Multiple stressors on coral reefs: A long-term perspective. Limnology and Oceanography. 44(3 (2)):932-940.

Hughes TP, Baird AH, Dinsdale EA, et al. 2012. Assembly Rules of Reef Corals Are Flexible along a Steep Climatic Gradient. Current Biology 22:736-741.

Hughes TP, Kerry JT, Alvarez-Noriega M, et al. 2017a. Global warming and recurrent mass bleaching of corals. Nature. 543(7645):373-377. https://doi.org/10.1038/nature21707

Hughes TP, Barnes ML, Bellwood DR, et al. 2017b. Coral reefs in the Anthropocene. Nature. 546(7656):82-90. https://doi.org/10.1038/nature22901

Hughes TP, Kerry JT, Baird AH, et al. 2018a. Global warming transforms coral reef assemblages. Nature. 556(7702):492-496. Supplementary Material. https://doi.org/10.1038/s41586-018-0041-2

Hughes TP, Anderson KD, Connolly SR, et al. 2018b. Spatial and temporal patterns of mass bleaching of corals in the Anthropocene. Science. 359(6371):80-83. https://www.science.org/doi/10.1126/science.aan8048

Hughes TP, Kerry JT, Connolly SR, et al. 2018c. Ecological memory modifies the cumulative impact of recurrent climate extremes. Nature Climate Change. 9(1):40-43. https://doi.org/10.1038/s41558-018-0351-2

Hughes TP, Kerry JT, Connolly SR, et al. 2021. Emergent properties in the responses of tropical corals to recurrent climate extremes. Current Biology 31, 1–7. https://doi.org/10.1016/j.cub.2021.10.046

IEA (International Energy Agency). 2018. Global energy and CO_2 status report- 2017. International Energy Agency. 2017 Report.

Iida Y, Takatani Y, Kojima, A et al. 2020. Global trends of ocean CO2 sink and ocean acidification: an observation-based reconstruction of surface ocean inorganic carbon variables. J Oceanogr https://doi.org/10.1007/s10872-020-00571-5

IPCC (Intergovernmental Panel on Climate Change). 2013. Climate Change 2013: The Physical Science Basis. Intergovernmental Panel on Climate Change. https://www.ipcc.ch/report/ar5/wg1/

IPCC (Intergovernmental Panel on Climate Change). 2018. Global Warming of 1.5°C: An IPCC Special Report. Intergovernmental Panel on Climate Change. https://www.ipcc.ch/sr15/

IPCC (Intergovernmental Panel on Climate Change). 2021. Climate Change 2021: The Physical Science Basis. Intergovernmental Panel on Climate Change. https://www.ipcc.ch/report/ar6/wg1/

IPCC (Intergovernmental Panel on Climate Change). 2022: Climate Change 2022: Impacts, Adaptation, and Vulnerability. Intergovernmental Panel on Climate Change. https://www.ipcc.ch/report/ar6/wg2/

Iguchi A, Kumagai NH, Nakamura T, et al. 2014. Responses of calcification of massive and encrusting corals to past, present, and near-future ocean carbon dioxide concentrations. Mar Pollut Bull 89:348-355.

Ishii M, Rodgers KB, Inoue HY, et al. 2020. Ocean acidification from below in the tropical Pacific. Global Biogeochemical Cycles 34, e2019GB006368. https://doi.org/10.1029/2019GB006368

Jackson J, Donovan M, Cramer K, et al. 2014. Staus and trends of Caribbean coral reefs 1970-2012. Gland, Switzerland: Global Coral Reef Monitoring Network.

Jiang LQ, Feely RA, Carter BR, et al. 2015. Climatological distribution of aragonite saturation state in the global oceans. Global Biogeochemical Cycles. 29(10):1656-1673. https://doi.org/10.1002/2015GB005198

Jones GP, McCormick MI, Srinivasan M, et al. 2004. Coral decline threatens fish biodiversity in marine reserves. PNAS 101 (21) 8251-8253.

Kahng SE, Addaynak D, Shlesinger T, et al. 2019. Light, temperature, photosynthesis, heterotrophy, and the lower depth limits of mesophotic coral ecosystems. In: Loya, Y., Puglise, K.A., Bridge, T.C.E. (eds.) Mesophotic Coral Ecosystems, p. 801-828. Springer.

Kamya PZ, Byrne M, Mos B, et al. 2017 Indirect effects of ocean acidification drive feeding and growth of juvenile crown-of-thorns starfish, Acanthaster planci. Proc. R. Soc. B 284: 20170778. http://dx.doi.org/10.1098/rspb.2017.0778

Kamya PZ, Byrne M, Mos B, et al. 2018. Enhanced performance of juvenile crown of thorns starfish in a warm-high CO2 ocean exacerbates poor growth and survival of their coral prey. Coral Reefs 37, 751–762. https://doi.org/10.1007/s00338-018-1699-5

Kang H, Chen X, Deng W, et al. 2021. Skeletal growth response of *Porites* coral to longterm ocean warming and acidification in the South China Sea. Journal of Geophysical Research: Biogeosciences, 126, e2021JG006423. https://doi.org/10.1029/2021JG006423

Kayal M, Vercelloni J, Wand MP, et al. 2015. Searching for the best bet in life-strategy: A quantitative approach to individual performance and population dynamics in reef-building corals. Ecological Complexity 23:73-84. https://doi.org/10.1016/j.ecocom.2015.07.003

Kayanne H, Suzuki R, Liu G. 2017. Bleaching in the Ryukyu Islands in 2016 and associated degree heating week threshold. Galaxea, Journal of Coral Reef Studies. 19:17-18. https://www.jstage.jst.go.jp/article/galaxea/19/1/19_17/_article

Keesing JK, Thomson DP, Haywood MDE, et al. 2019. Two time losers: selective feeding by crown-of-thorns starfish on corals most affected by successive coral-bleaching episodes on western Australian coral reefs. Mar Biol 166, 72 (2019). https://doi.org/10.1007/s00227-019-3515-3

Keesing, J.K., 2021. Optimal Foraging Theory Explains Feeding Preferences in the Western Pacific Crown-of-Thorns Sea Star *Acanthaster* sp. The Biological Bulletin, 241(3), pp.303-329.

Klein SG, Geraldi NR, Anton A, et al. 2022. Projecting coral responses to intensifying marine heatwaves under ocean acidification. Global Change Biology, 28, 1753– 1765. https://doi.org/10.1111/gcb.15818

Koido T, Oku Y, Fukuda M, et al. 2017. *Drupella* outbreak in a large coral community off the coast of Cape Toi, Miyazaki, Japan. Galaxea 19: 31-32. https://www.jstage.jst.go.jp/article/galaxea/19/1/19_31/_article

Kornder NA, Riegl BM, Figueiredo J. 2018. Thresholds and drivers of coral calcification responses to climate change. Glob Chang Biol. 24(11):5084-5095. https://doi.org/10.1111/gcb.14431

Kubomura T, Yamashiro H, Reimer JD. 2018. Appearance of an anomalous black band disease at upper mesophotic depths after coral bleaching. Diseases of Aquatic Organisms 131.3: 245-250. https://pubmed.ncbi.nlm.nih.gov/30459297/

Lamarck, JBP. 1816. Histoire naturelle des Animaux sans vertebres. Tome 2. (Verdi re: Paris). 568 p.

Lamb JB, Wenger AS, Devlin MJ, et al. 2016. Reserves as tools for alleviating impacts of marine disease. Phil. Trans. R. Soc. B 371:20150210. https://doi.org/10.1098/rstb.2015.0210

Lantz CA, Carpenter RC, Comeau S, et al. 2017. Organisms Composing an Experimental Coral Reef Community from Mo'orea, French Polynesia, Exhibit Taxon-Specific Net Production: Net Calcification Ratios. Front. Mar. Sci. 4:298. https://doi.org/10.3389/fmars.2017.00298

Lenihan HS, Holbrook SJ, Schmitt RJ, et al. 2011. Influence of corallivory, competition, and habitat structure on coral community shifts. Ecology 92: 1959–1971.

Lewis N, Day JC, Wilhelm A, et al. 2017. Large-scale marine protected areas: Guidelines for design and management. Best practice protected area guidelines series, no. 26. Gland, Switzerland: IUCN.

Logan CA, Dunne JP, Ryan JS, et al. 2021. Quantifying global potential for coral evolutionary response to climate change. Nat. Clim. Chang. 11, 537–542. https://doi.org/10.1038/s41558-021-01037-2

Longenecker K, Roberts TE, Colin PL. 2019. Papua New Guinea. In: Loya Y., Puglise K., Bridge T. (eds), Mesophotic Coral Ecosystems, p. 321 - 336. Springer.

Lough JM, Anderson KD, Hughes TP. 2018. Increasing thermal stress for tropical coral reefs: 1871-2017. Scientific Reports. 8(1):6079. https://doi.org/10.1038/s41598-018-24530-9

Loya Y, Eyal G, Treibitz T, et al. 2016. Theme section on mesophotic coral ecosystems: advances in knowledge and future perspectives. Coral Reefs 35:1–9. https://doi.org/10.1007/s00338-016-1410-7

Luzon KS, Lin M-F, Lagman MCA, et al. 2017. Resurrecting a subgenus to genus: molecular phylogeny of Euphyllia and Fimbriaphyllia (order Scleractinia; family Euphylliidae; clade V). PeerJ 5:e4074. https://doi.org/10.7717/peerj.4074

Magdaong ET, Fujii M, Yamano H, et al. 2013. Long-term change in coral cover and the effectiveness of marine protected areas in the Philippines: A meta-analysis. Hydrobiologia. 733(1):5-17.

Maynard J, van Hooidonk R, Eakin CM, et al. 2015. Projections of climate conditions that increase coral disease susceptibility and pathogen abundance and virulence. Nature Climate Change. 5:668-694. https://doi.org/10.1038/nclimate2625

MacNeil MA, Graham NA, Cinner JE, et al. 2015. Recovery potential of the world's coral reef fishes. Nature 520 (7547) 341-344. https://doi.org/10.1038/nature14358

MacNeil MA, Mellin C, Matthews S. et al. 2019. Water quality mediates resilience on the Great Barrier Reef. Nat Ecol Evol 3, 620–627. https://doi.org/10.1038/s41559-019-0832-3

Maggioni F, Pujo-Pay M, Aucan J, et al. 2021. The Bouraké semi-enclosed lagoon (New Caledonia) – a natural laboratory to study the lifelong adaptation of a coral reef ecosystem to extreme environmental conditions, Biogeosciences, 18, 5117–5140, https://doi.org/10.5194/bg-18-5117-2021.

Marcelino VR, Morrow KM, van Oppen MJH, et al. 2017. Diversity and stability of coral endolithic microbial communities at a naturally high pCO2 reef. Mol Ecol 19:5344-5357. https://doi.org/10.1111/mec.14268

Matear RJ, Lenton A. 2018. Carbon–climate feedbacks accelerate ocean acidification, Biogeosciences, 15, 1721–1732, https://doi.org/10.5194/bg-15-1721-2018

Matz MV, Treml EA, Haller BC. 2020. Estimating the potential for coral adaptation to global warming across the Indo-West Pacific. Glob Change Biol 26: 3473– 3481. https://doi.org/10.1111/gcb.15060

Mbaru EK, Graham NAJ, McClanahan TR, et al. Functional traits illuminate the selective impacts of different fishing gears on coral reefs. J Appl Ecol. 2020; 57: 241– 252. https://doi.org/10.1111/1365-2664.13547

McClanahan TR, Maina JM, Darling ES, et al. 2020. Large geographic variability in the resistance of corals to thermal stress. Global Ecol Biogeogr 29: 2229– 2247. https://doi.org/10.1111/geb.13191

McKenzie T, Habel S, Dulai H. 2021. Sea-level rise drives wastewater leakage to coastal waters and storm drains. Limnol Oceanogr Lett 6: 154-163. https://doi.org/10.1002/lol2.10186

McManus LC, Vasconcelos VV, Levin SA, et al. 2020. Extreme temperature events will drive coral decline in the Coral Triangle. Glob Change Biol 26: 2120– 2133. https://doi.org/10.1111/gcb.14972

Meron D, Maor-Landaw K, Eyal G, et al. 2020. The Complexity of the Holobiont in the Red Sea Coral *Euphyllia paradivisa* under Heat Stress. Microorganisms 3:372. https://doi.org/10.3390/microorganisms8030372

Milne Edwards H. 1860. Histoire Naturelle des Coralliaires ou Polypes Proprement Dits. Tome Troisieme. p.1-576. Librairie Encyclopédique de Roret, Paris.

Mollica NR, Guo W, Cohen AL, et al. 2018. Ocean acidification affects coral growth by reducing skeletal density. Proc Natl Acad Sci USA. 115(8):1754-1759. https://doi.org/10.1073/pnas.1712806115

Montgomery AD, Fenner D, Kosaki KK, et al. 2019. American Samoa. In: Loya Y, Puglise KA, Bridge T (eds), Mesophotic Coral Ecosystems, p. 387–407. Springer.

Montgomery AD, Fenner D, Donahue MJ, et al. 2021. Community similarity and species overlap between habitats provide insight into the deep reef refuge hypothesis. Sci Rep 11, 23787. https://doi.org/10.1038/s41598-021-03128-8

Morgan KM, Perry CT, Smithers SG, et al. 2016. Transitions in coral reef accretion rates linked to intrinsic ecological shifts on turbid-zone nearshore reefs. Geology 44: 995–998. https://doi.org/10.1130/G38610.1

Morgan KM, Perry CT, Johnson JA, et al. 2017. Nearshore Turbid-Zone Corals Exhibit High Bleaching Tolerance on the GBR Following the 2016 Ocean Warming Event. Frontiers in Marine Science 4:224. https://doi.org/10.3389/fmars.2017.00224

Moriarty T, Leggat W, Heron SF, Steinberg R, Ainsworth TD. 2023. Bleaching, mortality and lengthy recovery on the coral reefs of Lord Howe Island. The 2019 marine heatwave suggests an uncertain future for high-latitude ecosystems. PLOS Clim 2(4): e0000080. https://doi.org/10.1371/journal.pclm.0000080

MPA News. 2018. New Caledonia strengthens protection for reefs in its Coral Sea Natural Park. MPA News, September 2018, 20(2):7.

Muir PR, Wallace CC. 2016. A rare 'deep-water' coral assemblage in a shallow lagoon in Micronesia. Marine Biodiversity https://doi.org/10.1007/s12526-015-0419-4

Muir PR, Pichon M. 2019. Biodiversity of Reef-building, Scleractinian Corals. Pp 589–620 in: Loya Y, Puglise KA, Bridge T (eds), Mesophotic Coral Ecosystems. Springer.

Muir PR, Wallace C, Bridge TCL, et al. 2015. Diverse Staghorn Coral Fauna on the Mesophotic Reefs of North-East Australia. PLoS ONE 10(2). https://doi.org/10.1371/journal.pone.0117933

Muir PR, Marshall PA, Abdulla A, et al. 2017 Species identity and depth predict bleaching severity in reef-building corals: shall the deep inherit the reef ? Proc. R. Soc. B 284: 20171551. http://dx.doi.org/10.1098/rspb.2017.1551

Muir PR, Pichon M, Squire L Jnr, et al. 2019. *Acropora tenella*, a zooxanthellate coral extending to 110-m depth in the northern Coral Sea. Marine Biodiversity 49:809–814. https://doi.org/10.1007/s12526-018-0855-z

Muir PR, Obura DO, Hoeksema BW, et al. 2022. Conclusions of low extinction risk for most species of reef-building corals are premature. Nat Ecol Evol 6, 357–358. https://doi.org/10.1038/s41559-022-01659-5

NASEM (National Academies of Sciences, Engineering, and Medicine). 2019. A Research Review of Interventions to Increase the Persistence and Resilience of Coral Reefs. Washington, DC: The National Academies Press. https://nap.nationalacademies.org/catalog/25279/

NCEI (National Centers for Environmental Information). 2022. Climate at a Glance https://www.ncdc.noaa.gov/cag/ Global Time Series for ocean surface temperature anomalies, 1880 - 2020.

Nemenzo F. 1986. Guide to Philippine Flora and Fauna. Corals. Natural Resources Management Center and University of the Philippines. 273 pp.

Nicolet KJ, Chong-Seng KM, Pratchett MS. et al. 2018. Predation scars may influence host susceptibility to pathogens: evaluating the role of corallivores as vectors of coral disease. Sci Rep 8, 5258 https://doi.org/10.1038/s41598-018-23361-y

NMFS (National Marine Fisheries Service). 2012. Management report for 82 corals status review under the Endangered Species Act. NMFS Pacific Islands Regional Office, Honolulu, HI.

NMFS (National Marine Fisheries Service). 2014. Endangered and threatened wildlife and plants: Final listing determinations on proposal to list 66 reef building coral species and to reclassify elkhorn and staghorn corals. 79 FR 53851, September 10, 2014.

NMFS (National Marine Fisheries Service). 2020. Endangered and threatened wildlife and plants: Endangered Species Act Listing Determination for the Coral *Pocillopora meandrina*. 85 FR 40480, July 6, 2020.

NMFS (National Marine Fisheries Service). 2022a. Memo to file on international trade of Indo-Pacific coral genera and species listed under the ESA, based on CITES database. August 2022, NMFS Pacific Islands Regional Office, Honolulu, HI.

NMFS (National Marine Fisheries Service). 2022b. Records of ESA-listed Coral Species in U.S. Pacific Islands Waters and Application to Critical Habitat. June 2022, NMFS Pacific Islands Regional Office, Honolulu, HI.

NMFS (National Marine Fisheries Service). 2022c. Memo to file on Geographic distributions of ESA-listed corals in Veron's Corals of the World ecoregions (Veron et al. 2016) vs. Spalding et al.'s (2007) Marine Ecoregions of the World (MEOWs). September 7, 2022, NMFS Pacific Islands Regional Office, Honolulu, HI.

Nolan MKB, Schmidt-Roach S, Davis AR, et al. 2021. Widespread bleaching in the One Tree Island lagoon (Southern Great Barrier Reef) during record-breaking temperatures in 2020. Environ Monit Assess 193, 590. https://doi.org/10.1007/s10661-021-09330-5

NPSA (National Park of America Samoa). 2020. Excel spreadsheet (filename: NPSA_ESA_Coral_Distributions Depth Data thru 2019) provided by Eric Brown (NPSA) to Lance Smith (PIRO) in 2020.

Oberle FKJ, Storlazzi CD, Cheriton OM, et al. 2019. Physicochemical Controls on Zones of Higher Coral Stress Where Black Band Disease Occurs at Makua Reef, Kaua'i, Hawai'i. Front. Mar. Sci. 6:552. https://doi.org/10.3389/fmars.2019.00552

Oliver ECJ, Benthuysen JA, Darmaraki S, et al. 2021. Marine Heatwaves. Annual Review of Marine Science 13:313-342. https://doi.org/10.1146/annurev-marine-032720-095144

Ono H, Kosugi N, Toyama K, et al. 2019. Acceleration of ocean acidification in the Western North Pacific. Geophysical Research Letters, 46, 13,161–13,169. https://doi.org/10.1029/2019GL085121

Osman EO, Smith DJ, Ziegler M, et al. 2018. Thermal refugia against coral bleaching throughout the northern Red Sea. Glob Change Biol; 24: e474– e484. https://doi.org/10.1111/gcb.13895

Palumbi SR, Barshis DJ, Traylor-Knowles N, et al. 2014. Mechanisms of reef coral resistance to future climate change. Science 344(6186):895-8. https://www.science.org/doi/10.1126/science.1251336

Panchang, R. and Ambokar, M., 2021. Ocean acidification in the Northern Indian ocean: A review. Journal of Asian Earth Sciences, 219 https://doi.org/10.1016/j.jseaes.2021.104904

Pandolfi JM, Bradbury RH, Sala E, et al. 2003. Global trajectories of the long-term decline of coral reef ecosystems. Science. 301(5635):955-958.

Pavitt A, Malsch K, King E, et al. 2021. CITES and the sea: Trade in commercially exploited CITES-listed marine species. FAO Fisheries and Aquaculture Technical Paper No. 666. Rome, FAO. https://doi.org/10.4060/cb2971en

Pearson RG. 1981. Recovery and recolonization of coral reefs. Marine Ecology Progress Series 4:105-122.

Perry CT, Alvarez-Filip L, Graham NAJ, et al. 2018. Loss of coral reef growth capacity to track future increases in sea-level. Nature. 558(7710):396-400. https://doi.org/10.1038/s41586-018-0194-z

Pinheiro HT, Eyal G, Shepherd B, et al. 2019. Ecological insights from environmental disturbances in mesophotic coral ecosystems. Ecosphere 10(4):e02666. https://doi.org/10.1002/ecs2.2666

Plagányi ÉE, Babcock RC, Rogers J. et al. 2020. Ecological analyses to inform management targets for the culling of crown-of-thorns starfish to prevent coral decline. Coral Reefs 39, 1483–1499. https://doi.org/10.1007/s00338-020-01981-z

Ponti M, Fratangeli F, Dondi N, et al. 2016. Baseline reef health surveys at Bangka Island (North Sulawesi, Indonesia) reveal new threats. PeerJ. 2016 Oct 25;4:e2614. https://pubmed.ncbi.nlm.nih.gov/27812416/

Prasetia R, Sinniger F, Harii S. 2016. Gametogenesis and fecundity of *Acropora tenella* (Brook 1892) in a mesophotic coral ecosystem in Okinawa, Japan. Coral Reefs 35:53–62. https://doi.org/10.1007/s00338-015-1348-1

Prasetia R, Sinniger F, Harii S. 2017. First record of spawning in the mesophotic *Acropora tenella* in Okinawa, Japan. Galaxea 19:5–6. https://www.jstage.jst.go.jp/article/galaxea/19/1/19_5/_article/-char/ja/

Pratchett MS, Caballes CF, Wilmes JC, et al. 2017. Thirty Years of Research on Crown-of-Thorns Starfish (1986–2016): Scientific Advances and Emerging Opportunities. Diversity 9(4):41. https://doi.org/10.3390/d9040041

Pratchett MS, Caballes CF, Newman SJ, et al. 2020. Bleaching susceptibility of aquarium corals collected across northern Australia. Coral Reefs 39, 663–673. https://doi.org/10.1007/s00338-020-01939-1

Prouty NG, Cohen A, Yates KK, et al. 2017. Vulnerability of coral reefs to bioerosion from land-based sources of pollution. Journal of Geophysical Research: Oceans, 122, 9319–9331. https://doi.org/10.1002/2017JC013264

Putnam, HM. 2021. Avenues of reef-building coral acclimatization in response to rapid environmental change. J Exp Biol 224 (Suppl_1): jeb239319. doi: https://doi.org/10.1242/jeb.239319

Putnam HM, Barott KL, Ainsworth TD, et al. 2017. The vulnerability and resilience of reef-building corals. Current Biology. 27(11):R528-R540. https://doi.org/10.1016/j.cub.2017.04.047

PwC. 2017. The Long View. How will the global economic order change by 2050? www.pwc.com, 72 p.

Quelch JJ. 1886. Report on the Scientific Results of the Voyage of H.M.S. Challenger during the years 1873–1876. Zoology. 16 (46): 1-203, pl. 1-12.

Quimpo TJR, Requilme JNC, Gomez EJ, et al. 2020. Low coral bleaching prevalence at the Bolinao-Anda Reef Complex, northwestern Philippines during the 2016 thermal stress event. Marine Pollution Bulletin. 160. https://doi.org/10.1016/j.marpolbul.2020.111567

Randall RH, Myers RF. 1983. Guide to the Coastal Resources of Guam. Vol. 2. The Corals. University of Guam, Mangilao, Guam.

Raymundo, LJ, Burdick D, Hoot WC, et al. 2019. Successive bleaching events cause mass coral mortality in Guam, Micronesia. Coral Reefs 38:677–700. https://doi.org/10.1007/s00338-019-01836-2

Razak TB, Mumby PJ, Nguyen AD, et al. 2017. Use of skeletal Sr/Ca ratios to determine growth patterns in a branching coral Isopora palifera . Mar Biol 164, 96. https://doi.org/10.1007/s00227-017-3099-8

Rehberg H. 1892. Neue und venig bekannte Korallen. Abhandlungen der Naturwissenshaften Verin, Hamburg 12: 1-50.

Renzi JJ, Shaver EC, Burkepile DE, et al. 2022. The role of predators in coral disease dynamics. Coral Reefs 41, 405–422. https://doi.org/10.1007/s00338-022-02219-w

Richards ZT, van Oppen MJH, Wallace CC, et al. 2008. Some Rare Indo-Pacific Coral Species Are Probable Hybrids. PLoS ONE 3(9):e3240.

Richards ZT, van Oppen MJH, Wallace CC, et al. 2019. Correction: Some Rare Indo-Pacific Coral Species Are Probable Hybrids. PLoS ONE 14(1): e0211527. https://doi.org/10.1371/journal.pone.0211527

Richmond RH, Golbuu Y, Shelton AJ. 2019. Successful Management of Coral Reef-Watershed Networks. Editors: Wolanski E, Day JW, Elliott M, Ramachandran R. Coasts and Estuaries, p. 445-459. ISBN 9780128140031, https://doi.org/10.1016/B978-0-12-814003-1.00026-5.

Riegl BM, Glynn PW. 2020. Population dynamics of the reef crisis: Consequences of the growing human population. Edited by BM Riegl. Advances in Marine Biology 87, Issue 1: 1-30. https://doi.org/10.1016/bs.amb.2020.07.004.

Rinsky M, Weizman E, Ben-Asher HW, et al. 2022. Temporal gene expression patterns in the coral *Euphyllia paradivisa* reveal the complexity of biological clocks in the cnidarian-algal symbiosis. Sci Adv. 8(37):eabo6467. https://www.science.org/doi/10.1126/sciadv.abo6467

Robinson, JPW, JM McDevitt-Irwin, JC Dajka, et al. 2020. Habitat and fishing control grazing potential on coral reefs. Functional Ecology 34:240-251. https://doi.org/10.1111/1365-2435.13457

Rodríguez-Villalobos JC, Reyes-Bonilla H. 2019. History of perspectives on the study of coral disease in the eastern tropical Pacific. Dis Aquat Organ. 136(3):243-253. https://doi.org/10.3354/dao03411

Roff G, Mumby PJ. 2012. Global disparity in the resilience of coral reefs. Trends in Ecology and Evolution. 27(7):404-413.

Roff G, Clark TR, Reymond CE, et al. 2013. Palaeoecological evidence of a historical collapse of corals at Pelorus Island, inshore Great Barrier Reef, following European settlement. Proceedings of the Royal Society of London B. 280(1750):20122100.

Roff G, Chollett I, Doropoulos C, et al. 2015. Exposure-driven macroalgal phase shift following catastrophic disturbance on coral reefs. Coral Reefs. 34(3):715-725. https://doi.org/10.1007/s00338-015-1305-z

Rowley SJ, Roberts TE, Coleman RR, et al. 2019. Pohnpei, Federated States of Micronesia. In: Loya Y., Puglise K., Bridge T. (eds), Mesophotic Coral Ecosystems, p. 301 - 320. Springer.

Ruppert, JLW, Vigliola, L, Kulbicki, et al. 2018. Human activities as a driver of spatial variation in the trophic structure of fish communities on Pacific coral reefs. Glob Change Biol 24: e67– e79. https://doi.org/10.1111/gcb.13882

Sale PF, Szmant AM. 2012. Reef Reminiscences: Ratcheting back the shifted baselines concerning what reefs used to be. United Nations University Institute for Water, Environment and Health, Hamilton, ON, Canada, 35 pp.

Scaps P, Denis V, Berhimpon S, Runtukahu F. 2007. Zooxanthellate Scleractinian corals of the northern coast of Sulawesi. Atoll Research Bulletin 553:1-21.

Scheer G, Pillai CSG. 1974. Report on the Scleractinia of the Nicobar Islands. Results of the Xarifa Expedition 1957/1958 of the International Institute for Submarine Research, Vaduz, Lichtenstein (Director Dr. Hans Hass). Zoologica (Stuttgart) 42: 1-75.

Sheppard, C., Sheppard, A. and Fenner, D., 2020. Coral mass mortalities in the Chagos Archipelago over 40 years: regional species and assemblage extinctions and indications of positive feedbacks. Marine Pollution Bulletin, 154. https://doi.org/10.1016/j.marpolbul.2020.111075

Silapajarn K, Sulit VT, Tongdee N. 2017. Transforming Fisheries Development of Southeast Asia: SEAFDEC in Accord with the UN Sustainable Development Goals. Southeast Asian Fisheries Development Center. Fish for the People 15:1-15.

Sinniger F, Harii S. 2018. Studies on Mesophotic Coral Ecosystems in Japan. Pp 149-162 in: A. Iguchi, C. Hongo (eds.), Coral Reef Studies of Japan, Coral Reefs of the World 13. Springer.

Sinniger F., Morita M, Harii S. 2012. "Locally extinct" coral species *Seriatopora hystrix* found at upper mesophotic depths in Okinawa. Coral Reefs 32:153.

Sinniger F., Harii S, Humblet M, et al. 2019. Ryukyu Islands Japan. In: Loya Y., Puglise K., Bridge T. (eds), Mesophotic Coral Ecosystems, p. 231 - 248. Springer.

Skirving WJ, Heron SF, Marsh BL, et al. 2019. The relentless march of mass coral bleaching: a global perspective of changing heat stress. Coral Reefs 38, 547–557. https://doi.org/10.1007/s00338-019-01799-4

Slade LM, Kalangahe B. 2015. Dynamite fishing in Tanzania. Mar Pollut Bull. 101(2):491-6. https://doi.org/10.1016/j.marpolbul.2015.08.025

Smith TB, Maté JL, Gyory J. 2017. Thermal Refuges and Refugia for Stony Corals in the Eastern Tropical Pacific. In: Glynn, P., Manzello, D., Enochs, I. (eds) Coral Reefs of the Eastern Tropical Pacific. Coral Reefs of the World, vol 8. Springer, Dordrecht. https://doi.org/10.1007/978-94-017-7499-4_17

Smith JN, Mongin M, Thompson A, et al. 2020. Shifts in coralline algae, macroalgae, and coral juveniles in the Great Barrier Reef associated with present-day ocean acidification. Global Change Biology https://doi.org/10.1111/gcb.14985

Smith EG, Hazzouri KM, Choi JY, et al. 2022. Signatures of selection underpinning rapid coral adaptation to the world's warmest reefs. Science Advances 8 https://www.science.org/doi/10.1126/sciadv.abl7287

Spalding MD, Ravilious C, Green EP. 2001. World atlas of coral reefs. UNEP-WCMC, Cambridge.

Spalding MS, Fox HE, Allen GR. 2007. Marine Ecoregions of the World: A Bioregionalization of Coastal and Shelf Areas, BioScience 57:573–583. https://doi.org/10.1641/B570707

Speare,KE, Adam TC, Winslow EM, et al. 2022. Size-dependent mortality of corals during marine heatwave erodes recovery capacity of a coral reef. Global Change Biology, 28, 1342– 1358. https://doi.org/10.1111/gcb.16000

Steiner Z, Turchyn AV, Harpaz E, et al. 2018. Water chemistry reveals a significant decline in coral calcification rates in the southern Red Sea. Nat Commun. 9(1):3615. https://doi.org/10.1038/s41467-018-06030-6

Studer T. 1879. Zweite Abtheilung der Anthozoa Polyactinia, welche während der Reise A. M. S. Corvette Gazelle um die Erde gesammelt wurden. Monatsberichte der Königlich Preussischen Akademie der Wissenschaften zu Berlin. 1878: 525–550, pls. 1-5.

Sully S, van Woesik R. 2020. Turbid reefs moderate coral bleaching under climate-related temperature stress. Glob Change Biol; 26: 1367– 1373. https://doi.org/10.1111/gcb.14948

Swanson, D. 2019. Excel spreadsheet (filename: marian2017_AGLO_adultabd_estimatesv2) provided by Dione Swanson (PIFSC) to Lance Smith (PIRO) in April 2019. NMFS Pacific Islands Regional Office, Honolulu, HI.

Tamir, R., G. Eyal, N. Kramer, et al. 2019. Light environment drives the shallow-tomesophotic coral community transition. Ecosphere 10(9):e02839. https://doi.org/10.1002/ecs2.2839

Thangaradjou T, Machendiranathan M, Ranith R, et al. 2016. Coral disease prevalence in Gulf of Mannar and Lakshadweep Islands. Indian Journal of Geo Marine Sciences 45: 1755-1762.

Thinesh T, Meenatchi R, Jose PA, et al. 2019. Differential bleaching and recovery pattern of southeast Indian coral reef to 2016 global mass bleaching event: Occurrence of stress-tolerant symbiont *Durusdinium* (Clade D) in corals of Palk Bay. Mar Pollut Bull. 5:287-294. https://doi.org/10.1016/j.marpolbul.2019.05.033

Tkachenko KS, Hoang DT. 2022. Concurrent effect of crown-of-thorns starfish outbreak and thermal anomaly of 2020 on coral reef communities of the Spratly Islands (South China Sea). Marine Ecology, 43, e12717. https://doi.org/10.1111/maec.12717

Toonen R, Montgomery A. 2018. Mesophotic Corals of American Samoa: Implications for ESA-listed corals. Final report for NOAA Grant #NA15NOS4820082. Submitted to National Marine Fisheries Service, Pacific Islands Regional Office, Honolulu, HI.

Torda G, Sambrook K, Cross P, et al. 2018. Decadal erosion of coral assemblages by multiple disturbances in the Palm Islands, central Great Barrier Reef. Sci Rep 8, 11885. https://doi.org/10.1038/s41598-018-29608-y

Turak E, Sheppard C, Wood E. 2008. *Euphyllia paradivisa*. The IUCN Red List of Threatened Species 2008: e.T133057A3586802. https://dx.doi.org/10.2305/IUCN.UK.2008.RLTS.T133057A3586802.en

Turak E, Devantier L. 2012. Biodiversity and Conservation Priorities of Reef-building Corals in Timor Leste, with focus on the Nino Konis Santana National Marine Park. Final Report to Conservation International, 71 p.

Turak E, Devantier L. 2019. Reef building corals of the upper mesophotic zone of the Central Indo-West Pacific. In: Loya, Y., Puglise, K.A., Bridge, T.C.E. (eds.) Mesophotic Coral Ecosystems, p. 621-652. Springer.

Tuttle LJ, Donahue MJ. 2022. Effects of sediment exposure on corals: a systematic review of experimental studies. Environ Evid 11, 4. https://doi.org/10.1186/s13750-022-00256-0

UN (United Nations). 2015. Paris Agreement, 27 p. https://unfccc.int/files/essential_background/convention/application/pdf/english_paris_agreement.pdf

UN (United Nations). 2016. Paris Agreement Entry Into Force, 4 November 2016. 7 p. https://treaties.un.org/Pages/ViewDetails.aspx?src=TREATY&mtdsg_no=XXVII-7-d&chapter=27&clang=_en

UNEP (United Nations Environmental Programme). 2018. Emissions Gap Report 2018. United Nations Environmental Program. https://www.unenvironment.org/resources/emissions-gap-report-2018

UNEP (United Nations Environmental Programme). 2019. Emissions Gap Report 2019. United Nations Environmental Program. https://www.unenvironment.org/resources/emissions-gap-report-2019

UNEP (United Nations Environmental Programme). 2020. Emissions Gap Report 2020. United Nations Environmental Program. https://www.unep.org/emissions-gap-report-2020

UNEP (United Nations Environmental Programme). 2021a. Emissions Gap Report 2021. United Nations Environmental Program. https://www.unep.org/resources/emissions-gap-report-2021

UNEP (United Nations Environmental Programme). 2021b. Protected Planet Report 2020, updated May 2021. United Nations Environmental Program. https://livereport.protectedplanet.net/

UN-Habitat (United Nations Habitat Programme). 2015. Urbanization and Climate Change in Small Island Developing States. Nairobi, Kenya.

UNEP-WCMC. 2015. Review of corals from Fiji, Haiti, Solomon Islands and Tonga (coral species subject to EU decisions where identification to genus level is acceptable for trade purposes). UNEP-WCMC, Cambridge.

USGCRP (U.S. Global Change Research Program). 2018. 4th National Climate Assessment. https://nca2018.globalchange.gov/

van Hooidonk R, Maynard JA, Manzello D, et al. 2014. Opposite latitudinal gradients in projected ocean acidification and bleaching impacts on coral reefs. Global Change Biology. 20(1):103-112. https://doi.org/10.1111/gcb.12394

van Hooidonk R, Maynard J, Tamelander J, et al. 2016. Local-scale projections of coral reef futures and implications of the Paris Agreement. Sci Rep. 6:39666. https://doi.org/10.1038/srep39666

van Hooidonk R, Maynard J, Grimsditch G, et al. 2020. Projections of future coral bleaching conditions using IPCC CMIP6 models: climate policy implications, management applications, and Regional Seas summaries. United Nations Environment Programme, Nairobi, Kenya.

van Woesik R, Golbuu Y, Roff G. 2015. Keep up or drown: adjustment of western Pacific coral reefs to sea-level rise in the 21st century. R. Soc. open sci. 2: 150181. http://dx.doi.org/10.1098/rsos.150181

van Woesik R, Cacciapaglia CW. 2018. Keeping up with sea-level rise: Carbonate production rates in Palau and Yap, western Pacific Ocean. PLoS One. 13(5):e0197077. https://doi.org/10.1371/journal.pone.0197077

Vanhatalo J, Hosack GR, Sweatman H. 2017. Spatiotemporal modelling of crown-of-thorns starfish outbreaks on the Great Barrier Reef to inform control strategies. J Appl Ecol, 54: 188-197. https://doi.org/10.1111/1365-2664.12710

Vargas-Ángel B, Huntington B, Brainard RE, et al. 2019. El Niño-associated catastrophic coral mortality at Jarvis Island, central Equatorial Pacific. Coral Reefs 38, 731–741 (2019). https://doi.org/10.1007/s00338-019-01838-0

Vega Thurber R, Mydlarz LD, Brandt M, et al. 2020. Deciphering Coral Disease Dynamics: Integrating Host, Microbiome, and the Changing Environment. Front. Ecol. Evol. 8:575927. https://doi.org/10.3389/fevo.2020.575927

Veloria AI, Hernandez DT, Tapang GA, et al. 2021. Characterization of Open Water Explosions from Confiscated Explosives in the Philippines – Possible Implications to Local Marine Mammals. Science Diliman 33:5-21.

Vercelloni J, Caley MJ, Mengersen K. 2017. Crown-of-thorns starfish undermine the resilience of coral populations on the Great Barrier Reef. Global Ecol Biogeogr. 26: 846– 853. https://doi.org/10.1111/geb.12590

Veron JEN. 1986. Corals of Australia and the Indo-Pacific. Angus and Robertson, Sydney, 644 pp.

Veron JEN. 1990. New Scleractinia from Japan and other Indo-West Pacific countries. Galaxea 9: 95-173.

Veron JEN. 2000. Corals of the World. Australian Institute of Marine Science, 3 volumes.

Veron JEN. 2002. New species described in Corals of the World. Australian Institute of Marine Science, Monograph Serive Vol. 11, 212 p.

Veron JEN. 2014. Results of an update of the Corals of the World Information Base for theListing Determination of 66 Coral Species under the Endangered Species Act. Report to the Western Pacific Regional Fishery Management Council, Honolulu.

Veron JEN., Stafford-Smith MG, Turak E, DeVantier LM. 2016. Corals of the World, version 0.01. http://www.coralsoftheworld.org/page/home

Veron JEN, Pichon M. 1976. Scleractinia of Eastern Australia, Part I. Families Themnasteriidae, Astrocoendiidae, Pocilloporidae. Australian Institute of Marine Science Monograph Series, Vol. 1. 102 pp.

Veron JEN, Pichon M. 1980. Scleractinia of Eastern Australia, Part III. Families Agariciidae, Siderastreidae, Fungiidae, Oculinidae, Merulinidae, Mussidae, Pectiniidae, Caryophyllidae, Dendrophyllidae. Australian Institute of Marine Science Monograph Series, Vol. 4. 422 pp.

Veron JEN, Pichon M. 1982. Scleractinia of Eastern Australia, Part IV. Family Poritidae. Australian Institute of Marine Science Monograph Series, Vol. 5. 168 pp.

Veron JEN, Wallace CC. 1984. Scleractinia of Eastern Australia Part V. Family Acroporidae. Australian Institute of Marine Science Monograph Series, Vol. 6. 485 pp.

Veron JEN, Nishihira M. 1995. Corals of Japan. Kaiyusha Publishers Co., Ltd. 439 pp.

Veron JEN, Pichon M, Wijsman-Best M. 1977. Scleractinia of Eastern Australia Part II. Families Faviidae, Trachyphyliidae. Australian Institute of Marine Science Monograph Series, Vol. 3. 244 pp.

Veron JEN, Stafford-Smith M, DeVantier L, et al. 2015. Overview of distribution patterns of zooxanthellate Scleractinia. Frontiers in Marine Science. 1:1-19. https://doi.org/10.3389/fmars.2014.00081

Veron JEN, Stafford-Smith MG, Turak E, et al. 2016. Corals of the World. Accessed Jan-21, version 0.01. http://www.coralsoftheworld.org/

Verrill AR. 1902. Notes on the genus *Acropora* (*Madrepora* Lam.) with new descriptions and figures of types, and several new species. Transactions of the Connecticut Academy of Arts and Sciences 11: 207-66.

Vo ST, Phan KH, Hua TT, et al. 2019. Genus-specific bleaching at Con Dao Islands, Southern Vietnam. Galaxea, Journal of Coral Reef Studies 22: 27-28. https://doi.org/10.3755/galaxea.22.1_27

Waheed Z, Hoeksema BW. 2014. Diversity patterns of Scleractinian corals at Kota Kinabalu, Malaysia, in relation to exposure and depth. Raffles Bulletin of Zoology, 62: 66-82.

Wallace CC. 1978. The coral genus *Acropora* (Scleractinia: Astrocoeniidae: Acroporidae) in the central and southern Great Barrier Reef. Memoires of the Queensland Museum 8: 273-319.

Wallace CC. 1994. New species and a new species-group of the coral genus *Acropora* (Scleractinia: Astrocoeniina: Acroporidae) from Indo-Pacific locations. Invertebrate Taxonomy 8(4):961-988.

Wallace CC. 1999. Staghorn Corals of the World: A revision of the coral genus *Acropora* (Scleractinia: Astrocoeniidae: Acroporidae), with emphasis on morphology, phylogeny, and biogeography. CSIRO: Melborne. 421 pp.

Wallace CC, Wolstenholme J. 1998. Revision of the coral genus *Acropora* (Scleractinia, Astrocoeniinae, Acroporidae) in Indonesia. Zoological Journal of the Linnean Society 123: 199-384.

Wallace CC, Chen CA, Fukami H, et al. 2007. Recognition of separate genera within *Acropora* based on new morphological, reproductive and genetic evidence from *Acropora togianensis* and elevation of the subgenus *Isopora* Studer 1878 to genus. Coral Reefs 26: 231-239.

Wallace CC, Done BJ, Muir PR. 2012. Revision and catalogue of worldwide staghorn corals *Acropora* and *Isopora* (Scleractinia: Acroporidae) in the Museum of Tropical Queensland. Memoirs of the Queensland Museum - Nature 57:1-255.

Wells JW. 1954. Recent corals of the Marshall Islands. Professional Papers of the U.S. Geological Survey 260-I: 385-486.

Williams, ID, DJ White, RT Sparks, et al. 2016. Responses of Herbivorous fishes and benthos to 6 years of protection at the Kahekili Herbivore fisheries management area, Maui. PLoS One 11:e0159100. https://doi.org/10.1371/journal.pone.0159100

Williams ID, TL Kindinger, CS Couch, et al. 2019. Can Herbivore Management Increase the Persistence of Indo-Pacific Coral Reefs? Front. Mar. Sci. 6:557. https://doi.org/10.3389/fmars.2019.00557

Wilmes, J.C., Schultz, D.J., Hoey, A.S. et al. Habitat associations of settlement-stage crown-of-thorns starfish on Australia's Great Barrier Reef. Coral Reefs 39, 1163–1174 (2020). https://doi.org/10.1007/s00338-020-01950-6

Wooldridge SA. 2016. Excess seawater nutrients, enlarged algal symbiont densities and bleaching sensitive reef locations: 1. Identifying thresholds of concern for the GBR, Australia. Mar Pollut Bull. http://dx.doi.org/10.1016/j.marpolbul.2016.04.054

Yang SY, Lu CY, Tang SL, et al. 2020. Effects of Ocean Acidification on Coral Endolithic Bacterial Communities in *Isopora palifera* and *Porites lobata*. Front. Mar. Sci. 7:603293. https://doi.org/10.3389/fmars.2020.603293

Zhang J, Fenzhen S. 2020. Land Use Change in the Major Bays Along the Coast of the South China Sea in Southeast Asia from 1988 to 2018. Land 9, no. 1: 30. https://doi.org/10.3390/land9010030

Zuo X, Su F, Yu K, et al. 2021. Spatially Modeling the Synergistic Impacts of Global Warming and Sea-Level Rise on Coral Reefs in the South China Sea. Remote Sens. 13, 2626. https://doi.org/10.3390/rs13132626

Zweifler A, O'Leary M, Morgan K, et al. Turbid Coral Reefs: Past, Present and Future—A Review. Diversity. 2021; 13(6):251. https://doi.org/10.3390/d13060251

Zvuloni A, Artzy-Randrup Y, Katriel G, et al. 2015. Modeling the impact of white-plague coral disease in climate change scenarios. PLoS Comput Biol. 11(6):e1004151. https://doi.org/10.1371/journal.pcbi.1004151