Staghorn coral (*Acropora cervicornis*)
Elkhorn coral (*Acropora palmata*)
Lobed star coral (*Orbicella annularis*)
Mountainous star coral (*Orbicella faveolata*)
Boulder star coral (*Orbicella franksi*)
Rough cactus coral (*Mycetophyllia ferox*)
Pillar coral (*Dendrogyra cylindrus*)

5-Year Review:
Summary and Evaluation

National Marine Fisheries Service
Southeast Regional Office
Saint Petersburg, FL

January 2022

5-YEAR REVIEW

Species reviewed:

Staghorn coral (*Acropora cervicornis*)
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1.0 GENERAL INFORMATION

1.1 Reviewers

Lead Regional or Headquarters Office:
Southeast Regional Office - Alison Moulding, Ph.D., Protected Resources Division, 727-551-5607

Cooperating Science Center:
Southeast Fisheries Science Center - Mark Ladd, Ph.D., Population and Ecosystems Monitoring Division, 305-361-4200

1.2 Methodology used to complete review

This review was conducted by a two-person team with assistance from an undergraduate intern in the NOAA summer college internship program. Ciara Chen, a senior at Smith College, compiled literature published between 2014 and 2020 using online databases to identify relevant information for each of the ESA-listed species (Appendix 1). As the team became aware of new publications, they were incorporated into the review, but an extensive literature search was not conducted beyond 2020. In addition to published literature, unpublished information, and monitoring data were sought from the general public and the scientific and resource management communities through notification in the Federal Register, targeted emails to known coral monitoring programs, and a general email to the NOAA-sponsored Coral-List list server. Dr. Mark Ladd of the Southeast Fisheries Science Center graphed, analyzed, and summarized the monitoring data, and Dr. Alison Moulding of the Southeast Regional Office evaluated the literature and monitoring data and incorporated them into this 5-year review.

1.3 Background

1.3.1 FR Notice citation announcing initiation of this review

86 FR 1091, January 7, 2021

1.3.2 Listing History

Original Listing
FR notice: 71 FR 26852
Date listed: May 9, 2006
Entity listed:
Staghorn coral (*Acropora cervicornis*)
Elkhorn coral (*Acropora palmata*)
Classification: Threatened

FR notice: 79 FR 53852
Date listed: September 10, 2014
Entity listed:
Lobed star coral (*Orbicella annularis*)
Mountainous star coral (*Orbicella faveolata*)
Boulder star coral (*Orbicella franksi*)
Rough cactus coral (*Mycetophyllia ferox*)
Pillar coral (*Dendrogyra cylindrus*)
Classification: Threatened

Revised Listing
FR notice: 79 FR 53852
Date listed: September 10, 2014
Entity listed:
Staghorn coral (*Acropora cervicornis*)
Elkhorn coral (*Acropora palmata*)
Classification: Threatened

1.3.3 Associated rulemakings

4(d) Rule
FR Notice: 73 FR 64264, October 29, 2008 (staghorn and elkhorn corals)

Critical Habitat Designation
FR Notice: 73 FR 72210, November 26, 2008 (staghorn and elkhorn corals)

Proposed Critical Habitat
FR Notice: 85 FR 76302, November 27, 2020 (lobed star coral, mountainous star coral, boulder star coral, pillar coral, rough cactus coral)

1.3.4 Review History

Prior to listing, status reviews were conducted for elkhorn and staghorn corals in 2005 and for the other five species in 2011. This is the first 5-year review of mountainous star coral, lobed star coral, boulder star coral, pillar coral, and rough cactus coral since their listing as threatened in 2014. Elkhorn coral and staghorn coral were last reviewed in 2014 at the time of listing of the other five coral species and reaffirmed as threatened.

Acropora Biological Review Team. 2005. Atlantic *Acropora* Status Review Document. Report to National Marine Fisheries Service, Southeast Regional Office. March 3, 2005. 152 p + App.

Brainard, R.E., C. Birkeland, C.M. Eakin, P. McElhany, M.W. Miller, M. Patterson, and G.A. Piniak. 2011. Status review report of 82 candidate coral species petitioned under the U.S. Endangered Species Act. U.S. Dep. Commer., NOAA Tech. Memo., NOAA-TM-NMFS-PIFSC-27, 530 p. +1 Appendix.

1.3.5 Species' Recovery Priority Number at start of 5-year review

3C as indicated in the Recovering Threatened and Endangered Species FY 2019-2020 Report to Congress.

Demographic Risk: Moderate because listed as Threatened and is at or below depensation, has fragmented distribution, and decreasing trend.

Major Threats Understood: Multiple threats include climate change, land-based sources of pollution, trophic effects of fishing, diseases, and depensatory effects.

U.S. Jurisdiction Exists: United States has the authority and ability to address all of the major threats, perhaps except diseases and depensatory effects.

Action will be Effective: While actions to abate climate change are difficult, they will be extremely effective. Actions to abate other threats, such as watershed management and reduction of overharvest of herbivores will also be effective. Novel recovery actions such as propagation of resilient genotypes are proving to be effective too.

Conflict: The species are in conflict with construction, development, or other forms of economic activity.

1.3.6 Recovery Plan or Outline

Name of plan or outline: Recovery Plan for Elkhorn Coral (*Acropora palmata*) and Staghorn Coral (*Acropora cervicornis*)
Date issued: March 2015
Dates of previous revisions, if applicable: N/A

Name of plan or outline: Recovery Outline for Pillar Coral, Rough Cactus Coral, Lobed Star Coral, Mountainous Star Coral, and Boulder Star Coral
Date issued: March 2015
Dates of previous revisions, if applicable: N/A

2.0 REVIEW ANALYSIS

2.1 Application of the 1996 Distinct Population Segment (DPS) policy

2.1.1 Is the species under review a vertebrate?

______**Yes**, *go to section 2.1.2*
__X_ **No**, *go to section 2.2*

2.1.2 Is the species under review listed as a DPS?

______**Yes**, *give date and go to section 2.1.3.1*
______**No**, *go to section 2.1.4*

2.1.3 Was the DPS listed prior to 1996?

_____**Yes**, *go to section 2.1.2*
_____**No**, *go to section 2.2*

2.1.3.1 Prior to this 5-year review, was the DPS classification reviewed to ensure it meets the 1996 policy standards?

_____**Yes**, *provide citation and go to section 2.1.4*
_____**No**, *go to section 2.1.3.2*

2.1.3.2 Does the DPS listing meet the discreteness and significance elements of the 1996 DPS policy?

_____**Yes**, *discuss how it meets the DPS policy, and go to section 2.1.4*
_____**No**, *discuss how it is not consistent with the DPS policy and consider the 5-year review completed. Go to section 2.4., Synthesis.*

2.1.4 Is there relevant new information for this species regarding the application of the DPS policy?

_____**Yes**, *provide citation(s) and a brief summary of the new information; explain how this new information affects our understanding of the species and/or the need to list as DPSs. This may be reflected in section 4.0, Recommendations for Future Actions. If the DPS listing remains valid, go to section 2.2, Recovery Criteria. If the new information indicates the DPS listing is no longer valid, consider the 5-year review completed, and go to section 2.4, Synthesis.*
_____**No**, *go to section 2.2., Recovery Criteria*

2.2 Recovery Criteria

2.2.1 Does the species have a final, approved recovery plan containing objective, measurable criteria?

Elkhorn coral and staghorn coral have a recovery plan with objective, measurable criteria, some of which are interim criteria. The other five coral species do not have a recovery plan with criteria.

2.2.2 Adequacy of recovery criteria.

2.2.2.1 Do the recovery criteria reflect the best available and most up-to date information on the biology of the species and its habitat?

__X__**Yes**, *go to section 2.2.2.2*
_____**No**, *go to section 2.2.3, and note why these criteria do not reflect the best available information. Consider developing recommendations for revising recovery criteria in section 4.0.*

2.2.2.2 Are all of the 5 listing factors that are relevant to the species addressed in the recovery criteria (and is there no new information to consider regarding existing or new threats)?

_____**Yes**, *go to section 2.2.3*
__X__**No**, *go to section 2.2.3, and note which factors do not have corresponding criteria. Consider developing recommendations for revising recovery criteria in section 4.0.*

2.2.3 List the recovery criteria as they appear in the recovery plan, and discuss how each criterion has or has not been met, citing information.

All recovery criteria below are for staghorn and elkhorn coral. The other five coral species do not have recovery criteria.

Criterion 1: Abundance
Elkhorn coral: *Thickets are present throughout approximately 10 percent of consolidated reef habitat in 1 to 5 m water depth within the forereef zone. Thickets are defined as either a) colonies ≥ 1 m diameter in size at a density of 0.25 colonies per m*^{2} *or b) live elkhorn coral benthic cover of approximately 60 percent. Populations with these characteristics should be present throughout the range and maintained for 20 years;*

and

Staghorn coral: *Thickets are present throughout approximately 5 percent of consolidated reef habitat in 5 to 20 m water depth within the forereef zone. Thickets are defined as either a) colonies ≥ 0.5 m diameter in size at a density of 1 colony per m*^{2} *or b) live staghorn coral benthic cover of approximately 25 percent. Populations with these characteristics should be present throughout the range and maintained for 20 years.*

Neither of these abundance criteria have been met as thickets are rarely encountered throughout the species' ranges.

Criterion 2: Genotypic Diversity
Maintain current overall average genotypic diversity (proportion of unique genotypes per number of colonies sampled) of approximately 0.5 across these species' range.

Genotypic diversity has remained approximately 0.5 across the range though can vary substantially at individual sites. For instance, some reefs have very low genotypic diversity such as *A. palmata* in the Florida Keys (Baums et al. 2005a; Baums et al. 2005b).

Criterion 3: Recruitment
Observe recruitment rates necessary to achieve Criteria 1 and 2 over approximately 20 years;

and

Observe effective sexual recruitment (i.e., establishment of new larval-derived colonies and survival to sexual maturity) in each species' population across their geographic range.

This criterion has not been met. Observed sexual recruitment of staghorn and elkhorn corals is virtually absent throughout their ranges.

Interim Criterion 4: Disease (Listing Factor C)

Develop a quantitative recovery criterion through research. Based on 5 years of data on disease prevalence and amount of partial and total colony mortality in extant thickets, a criterion will be established to identify disease carrying capacity and to reduce the impact of disease to a level appropriate for recovery.

Although this criterion is interim, disease is still a major threat to these two species as discussed in the next section.

Criterion 5: Local and Global Impacts of Rising Ocean Temperature and Acidification (Listing Factor E)

Sea surface temperatures across the geographic range have been reduced to Degree Heating Weeks less than 4;

and

Mean monthly sea surface temperatures remain below 30°C during spawning periods;

and

Open ocean aragonite saturation has been restored to a state of greater than 4.0, a level considered optimal for reef growth.

This criterion has not been met. Ocean warming and aragonite saturation are tied to greenhouse gas emissions and climate change, which have progressed without slowing down as discussed in the next section.

Criterion 6: Loss of Recruitment Habitat (Listing Factor A)

Abundance (Criterion 1 above) addresses the threat of Loss of Recruitment Habitat because the criterion specifies the amount of habitat occupied by the two species. If Criterion 1 is met, then this threat is sufficiently abated;

or

Throughout the ranges of these two species, at least 40 percent of the consolidated reef substrate in 1-20 m depth within the forereef zone remains free of sediment and macroalgal cover as measured on a broad reef to regional spatial scale.

This criterion has not been met as remnant thickets are observed in only a small number of locations and do not fulfill the habitat occupancy level identifies in Criterion 1. Additionally, as coral communities continue to decline, the available space on the reef becomes occupied by faster recruiting organisms such as macroalgae (Hughes 1994).

Interim Criterion 7: Nutrients, Sediments, and Contaminants (Land Based Sources of Pollution) (Listing Factor E)

Develop quantitative recovery criteria through research. Based on 5 years of data, criteria will be established to reduce sources of nutrients, sediments, and contaminants to levels appropriate for recovery.

Although this is an interim criterion, nutrients, sediments, and contaminants continue to be a threat to these species as discussed in the next section.

Criterion 8: Regulatory Mechanisms (Listing Factor D)
Adequate domestic and international regulations and agreements are adopted as applicable to ensure that all threat-based criteria are met. For example, appropriate local, state/regional, national, international, and multi-jurisdictional efforts, agreements, and regulations are necessary to abate the threats from LBSP, physical impacts to corals, and rising sea surface temperatures and ocean acidification resulting from increasing atmospheric CO_2 *concentrations.*

As none of the threat-based criteria have been met, existing regulatory mechanisms are not sufficient. This criterion has not been met.

Criterion 9: Natural and Anthropogenic Abrasion and Breakage (Listing Factor E)
Appropriate and effective regulatory, response, restoration, and enforcement mechanisms are in place domestically and internationally for both planned and unplanned impacts. For planned impacts (e.g., marine construction), project planning should ensure no net loss of listed corals. Where natural or anthropogenic impacts do occur, an effective and complete response plan, including appropriate compensatory and site restoration, is executed.

Regulatory, response, restoration, and enforcement mechanisms are in place domestically for unplanned events. This criterion has not been met internationally or for planned projects domestically.

Interim Criterion 10: Predation (Listing Factor C)
Develop a quantitative recovery criterion through research. Based on 5 years of data on predation prevalence and amount of mortality in extant thickets, a criterion will be established to identify predation carrying capacity and to reduce the impact of predation to a level appropriate for recovery.

Although this criterion is interim, predation continues to be a threat to these two species as discussed in the next section.

2.3 Updated Information and Current Species Status

2.3.1 ACROPORA CERVICORNIS

2.3.1.1 Biology and Habitat

2.3.1.1.1 New information on the species' biology and life history:

In a study of larval longevity and competency, Miller et al. (2020a) found that in the absence of settlement cues, there was high *A. cervicornis* larval mortality through 4-5 days after spawning and that metamorphosis began on days 10-11 after spawning. Onset of settlement in the presence of settlement cues began at 3-4 days after spawning with rates increasing at 6-8 days and peaking at 8-15 days (Miller et al. 2020a).

There have been new studies of growth and calcification of *A. cervicornis*. In a study of naturally occurring, unattached fragments in Puerto Rico that were followed for 18 months, survivorship did not exceed 26%. Fragments had relatively low growth rates (average between 0.02 and 0.09 cm d^{-1}) and did not produce branches (Mercado-Molina et al. 2014). In contrast, in a study of 1,700 *A. cervicornis* fragments in nurseries in Florida and the Dominican Republic, high survivorship and increased growth after intentional fragmentation for propagation was observed in colonies that lost as much as 95% of their tissue (Lirman et al. 2014). Greater than 5 cm of new coral was produced annually for every existing 1 cm of coral. Additionally, this study found a positive relationship between size and growth but a decreasing rate of productivity with increasing size.

In a 6 month study of growth and calcification of *A. cervicornis* fragments grown in a nursery in the Florida Keys, colonies grown on the benthos had a lower rate of linear extension and higher skeletal density than *A. cervicornis* colonies grown suspended in the water column (Kuffner et al. 2017). Calcification rates did not differ between the two methods but did vary between genotypes, suggesting a genetically based variability in calcification rates (Kuffner et al. 2017). Similarly, genotypic differences in growth rates were observed among 37 genotypes of *A. cervicornis* grown in common garden environments in nurseries in Florida and the Dominican Republic, with fast-growing genotypes growing up to an order of magnitude faster than slower-growing genotypes (Lirman et al. 2014). Another study found genotypic differences in growth rates in nurseries were not predictive of growth rates after outplanting for restoration (O'Donnell et al. 2018).

Corals have associated microbiota comprised of a diverse consortium of organisms, including bacteria, which reside in the surficial mucus layer and are important for coral health, but remain poorly understood. The microbiome of *A. cervicornis* was shown to be dominated by Rickettsiales-like bacterium both in corals sampled at different depths in northeast Puerto Rico (Godoy-Vitorino et al. 2017) and in corals grown in a common nursery in the Cayman Islands (Miller et al. 2020b). There were significant differences in the abundance of less dominant taxa at different water depths (Godoy-Vitorino et al. 2017) and in the microbial communities among genotypes, but not within different sample locations in the same colony (Miller et al. 2020b).

2.3.1.1.2 Abundance, population trends (e.g. increasing, decreasing, stable), demographic features (e.g., age structure, sex ratio, family size, birth rate, age at mortality, mortality rate, etc.), or demographic trends:

There have been new publications on previously undocumented *A. cervicornis* thickets or surveys of known thickets. A survey of Pedro Bank, Jamaica recorded a single area within the proposed fishery reserve with extensive *A. cervicornis* thickets (Bruckner et al. 2014). At Coral Gardens, Belize, 9 of 11 areas predicted from satellite imagery to contain *Acropora* spp. were found to contain *Acropora* (Busch et al. 2016). Overall, 7.6 ha of the shallow (<7 m) reef crest and backreef area in Belize were dominated by *Acropora* spp., which is one of the largest populations identified in the Caribbean. Lagoonal areas containing *Acropora* spp. were dominated by *A. cervicornis,* while reef crests were dominated by *A. palmata*. The largest thickets were about 2 ha in size, and the smallest were scattered isolated thickets of a few square meters. The average cover was 53% live monospecific *A. cervicornis*, ranging from 28-64% (Busch et al. 2016).

In surveys of the nearshore ridge complex from Hillsboro to Port Everglades conducted in 2011-2013 in southeast Florida, *A. cervicornis* was present in 48% of the 1,956 sites (5000 m^2 each) (D'Antonio et al. 2016). Using the average colony size of 30 x 30 cm^2 (900 cm^3), *A. cervicornis* was abundant (>150 occurrences) at 11% of the sites, common (51-150 occurrences) at 11% of the sites, frequent (31-50 occurrences) at 5% of the sites, occasional (11-30 occurrences) at 8% of the sites, and rare (1-10 occurrences) at 13% of the sites. *A. cervicornis* was most frequently found at sites dominated by hardbottom (26%) and rubble (12%), and abundant populations tended to occur along the western edge of the ridge crest (D'Antonio et al. 2016).

Other studies examined how coral colony density can influence the survival and growth of colonies. Surveys of wild and outplanted *A. cervicornis* found that high density stands may promote a positive feedback by providing shelter for fish, which in turn, provide nutrients back to the coral and can fuel faster growth (Huntington et al. 2017). There may be a threshold density where positive feedbacks are initiated that can promote the growth and survival of outplanted *A. cervicornis* (Ladd et al. 2016). However, high coral colony density can result in higher prevalence of predation and disease and lower growth and survival in corals outplanted for restoration (Goergen and Gilliam 2018; Ladd et al. 2016).

Several studies or monitoring programs have documented temporal changes in percent cover of *A. cervicornis*. A study at Dairy Bull Reef off the northern coast of Jamaica found that cover of *A. cervicornis* increased from 2% to 22% from 2006 to 2008 (Crabbe 2014). Unpublished monitoring data from the Southeast Florida Coral Reef Evaluation and Monitoring Program (SECREMP) and the Coral Reef Evaluation and Monitoring Program (CREMP) in Florida show an overall decline in percent cover and live tissue area of *A. cervicornis* in permanent monitoring stations in the Dry Tortugas, Florida Keys, and southeast Florida between 2014 and 2019 (Appendix 2, Figures 1 and 4). Declines were apparent at both the regional and state-wide level, though there was variability at individual sites (Appendix 2, Figures 1-5). Across all 260 transects surveyed, the mean percent cover of *A. cervicornis* decreased by an order of magnitude from 0.04% in 2014 to 0.003% in 2019. In contrast, at monotypic and special habitat sites in the Dry Tortugas, Florida, there was an increase in total live area of *A. cervicornis* between 2014 and 2019 (Appendix 2, Figure 6).

Density and abundance have also generally declined in Florida. Unpublished CREMP and SECREMP data show mean density of *A. cervicornis* in Florida decreased 4-fold from 2014 to 2019 (0.017 colonies m^{-2} versus 0.004 colonies m^{-2}; Appendix 2, Figure 7). However, patterns in mean density varied among regions. In the Dry Tortugas, the mean density of *A. cervicornis* colonies was variable but remained relatively similar in 2014 and 2019 (Appendix 2, Figure 7). In contrast, the mean density of *A. cervicornis* in the Florida Keys decreased from 0.021 colonies m^{-2} in 2014 to 0.003 colonies m^{-2} in 2019 (Appendix 2, Figure 7). Similarly, the mean density of *A. cervicornis* on transects in southeast Florida decreased from 0.01 colonies m^{-2} in 2014 to 0.005 colonies m^{-2} in 2019 (Appendix 2, Figure 7). However, at monotypic and special habitat sites in the Dry Tortugas, density increased between 2014 and 2019 from 0.5 to 0.9 colonies m^{-2} (Appendix 2, Figure 9). In a separate monitoring study in southeast Florida, abundance of *A. cervicornis* colonies decreased between 2015 and 2020, particularly between 2017 and 2018, but the number of larger colony masses (area of coral where individual colonies are indistinguishable) remained stable (Appendix 2, Figures 17 and 18).

There have been new publications on coral demographics and population modeling. A survey of two *A. cervicornis* thickets over 8 years in southeast Florida showed temporal variability in mean percent cover but an overall loss of more than 50% (reduction from 17 to 3% at one site and 26 to 7% at the other) (Goergen et al. 2019). Disturbances including hurricanes, tropical storms, and disease events caused widespread and prolonged mortality; periods without disturbances allowed for recovery and growth. Predation was chronic and may have implications for reproduction, growth, and disease transmission, but less mortality resulted from predation compared to disease, which was constantly present and increased during the summer. Disease prevalence was higher during high water temperature events, after storms, and on larger colonies. Fragmentation rates were not high enough to replace losses from disturbance events. The authors conclude that a more substantial amount of time between disturbance events than experienced during the study is necessary to allow for species growth and recovery and is unlikely until climate change and ocean warming are addressed.

Seasonal surveys of 5,515 *A. cervicornis* colonies were conducted at 11 sites among three regions of Florida (Broward, middle Keys, and Dry Tortugas) from 2011 to 2015 (Goergen et al. 2020). There were differences in distribution among the regions. Sites in the northern region had cover from nearly 100% to sporadic colonies in low density on the periphery of the sites; the two other regions typically had sporadic clusters of low to moderate densities separated by tens of meters. Based on colony size, the proportion of colonies of reproductive size (>30 cm) was 60-80% in the northern region, 43-60% in the middle region, and 45-65% in the southern region. Overall, the mean colony maximum diameter was 44 cm with live tissue covering 72% of the colony. Recent mortality affected 17% of colonies surveyed with an average of 8% of tissue loss per colony. Disease caused the largest amount of tissue loss per colony in all regions. Prevalence of predation by fireworms and snails was twice as high in the middle region as in the other two regions, and damselfish predation prevalence was four times higher in the southern region of the Dry Tortugas than in the middle Keys and Broward. Mean diameter of colonies decreased from north to south, but the most southern region had on average a higher amount of live tissue per colony than the middle region. From the start to the end of the survey, mean colony diameter increased by 9% in the middle region and 22% in the southern region but decreased 1% in the northern region. However, changes in size class distribution were rarely observed.

In northeast Puerto Rico, a demographic model was developed by following 300 wild *A. cervicornis* colonies (no thickets; mean colony height 19-23 cm) from 2011 to 2013 at two locations (Mercado-Molina et al. 2015a). The model was used to perform a population viability analysis. Colony survival was between 88 and 89% during the first year; population growth decreased by 23 and 38% during the second year. There was a population decline ($\lambda<1$) at both sites due to the lack of sexual recruitment, relatively low rates of colony fragmentation, and the combination of lower colony survival, little colony growth, and higher levels of colony shrinkage. The low probability of larger-sized colonies surviving and remaining in the largest size class was the demographic transition that contributed most to the temporal reduction in λ. The viability analysis predicted the populations would reach a quasi-extinction level of 25% of the initial population size in ≤16 years and become functionally extinct (10% of the initial population size) in ≤20 years. However, transplanting at least 50 colonies of small sized colonies (≤100 cm total linear length) per year was enough to keep the population growth rate positive.

Another analysis using the same two populations of *A. cervicornis* in northeastern Puerto Rico as described above found that colony growth was more likely to occur when partial colony mortality was ≤20% (Mercado-Molina et al. 2018). This was consistent among different size classes. Analysis indicated that colonies with 20% or less partial mortality were between 6.5

and 28.7 times more likely to survive than colonies with higher partial mortality. In simulations, increasing the number of colonies with partial mortality by 25% during each time step caused the populations to reach a quasi-extinction level of 25% of the initial population size 3-4 years sooner.

A population dynamics study of *A. cervicornis* colonies experiencing shut down reaction disease (spontaneous disintegration of the tissue that can kill a coral quickly) in Puerto Rico found that the disease was more likely to affect smaller colonies less than 100 cm total linear length (Mercado-Molina et al. 2020). The disease affected 78% of the colonies within 6 months. Models indicated that at the population growth rate observed, extinction of the population could occur within 5 years and that disease incidence as low as 5% could cause the population to reach a pseudo-extinction level of 10% of the initial population size in 17 years and reach extinction in 33 years.

2.3.1.1.3 Genetics, genetic variation, or trends in genetic variation (e.g., loss of genetic variation, genetic drift, inbreeding, etc.):

There have been new studies examining the genetics of *A. cervicornis*. A study of Florida *A. cervicornis* found high genetic diversity along the Florida reef tract and within each regional population (Drury et al. 2016). There was also extensive regional population structure for Florida *A. cervicornis* with the highest diversity in the northern and southern portion of the reef tract (Drury et al. 2017b). In contrast, genetic diversity within thickets at Cordelia Bank, Honduras was low across three banks (genetic similarity 91-96% between banks) (Canty et al. 2021).

Several studies have examined genotypic diversity of thickets and isolated colonies. High density thickets in Florida and the Dominican Republic were composed of 13 to 30 genotypes per site, but 47% of genotypes were also found as isolated discrete colonies outside of the aggregations (Drury et al. 2019). Although genotypic diversity was higher in plots with isolated colonies (0.45 - 0.71) than thickets, few genets were found exclusively as isolated, discrete colonies (Drury et al. 2019). Thickets at Cordelia Bank in Honduras were made up of multiple genotypes (161 genotypes out of 205 samples = 0.79 genotypic diversity) that did not overlap between banks (Canty et al. 2021).

In a study of three reef sites (Coral Gardens, Rocky Point, Manatee Channel) off of Ambergris Caye, Belize, genotypic diversity varied from 0.05 at Coral Gardens (previously identified as one of the largest stands in the Caribbean) to 0.42 at Manatee Channel (Irwin et al. 2017). When pooled, there was low genotypic diversity (0.08) indicating predominantly asexual recruitment. The study also examined the age of five of the genets at Coral Gardens using somatic mutation rates and found the minimum age of 62–409 years, indicating the genets persisted during the 1980s species collapse and that this site may be a refuge for *A. cervicornis*. No somatic mutations were observed for any *A. cervicornis* at Manatee Channel, indicating the genets may be of more recent origin.

Very few colonies of *A. cervicornis* were encountered on Guadeloupian reefs, but one unique site (Caye-à-Dupont) contained a dense population (Japaud et al. 2015). In 80 samples collected within a circular plot of 30 m radius, one genotype was detected (genotypic diversity = 0.0125). This indicates that maintenance of this population is primarily asexual with limited sexual recruitment.

2.3.1.1.4 Spatial distribution, trends in spatial distribution (e.g. increasingly fragmented, increased numbers of corridors, etc.), or historic range (e.g. corrections to the historical range, change in distribution of the species' within its historic range, etc.):

There were new publications on surveys targeting the presence and distribution of *A. cervicornis*. In a survey of 37 sites along the terrace edge (9-15 m depth) interspersed among 7 of the main reef systems in Cuba (Havana, Artemisa, Los Colorados, Punta Francés, Los Canarreos Archipelago, Península Ancón, and Jardines de la Reina) conducted between 2010 and 2016, *A. cervicornis* was virtually absent (González-Díaz et al. 2018). In surveys of the forereef and reef crest of Jardines de la Reina National Park in Cuba (about 55 linear km surveyed) in 2017, 252 colonies of *A. cervicornis* were observed (Hernandez-Fernandez et al. 2019). Of these colonies, 30% had recent mortality affecting >16% of the colony. Old mortality was present in 52% of colonies, and disease was present in 0.6%.

In a survey of potential *Acropora* spp. habitat between 2016 and 2018 at seven locations (24 reefs) in Colombia along a latitudinal gradient on the continental coastline and insular area of San Andres, small patches in "good" condition were only present at two locations (García-Urueña and Garzón-Machado 2020). *Acropora cervicornis* colonies were dispersed with the abundance of patches and the highest cover observed around the Urabá Gulf and the Rosario Islands; cover was lower than 10%, and few healthy colonies were observed. Small (<30 cm^2) colonies predominated in all locations, and percent cover was generally low with an average of 6% and ranging from less than 4% to 11%. Larger colonies did not exceed 160 cm^2. Although disease was not observed, only three locations out of the six containing *A. cervicornis* had >50% of the populations rated as "healthy." The other half of the locations had between 28 and 38% of the populations rated as "healthy." The authors note widespread and severe declines compared to previous surveys; *A. cervicornis* is much reduced at many locations and nearly absent from one location where it was previously found (García-Urueña and Garzón-Machado 2020).

In a survey of 52 stations in St. Croix in 2007 and 52 stations in St. Thomas and St. John in 2009, *A. cervicornis* was observed at 2% of stations in St. Croix and 19% of stations in St. Thomas and St. John (Fisher et al. 2014).

Unpublished benthic monitoring data from the National Coral Reef Monitoring Program (NCRMP) show that in surveys conducted between 2014 and 2020 using a stratified random sample design (different sites visited each year), *A. cervicornis* was present at only a small percentage of the sites visited in Florida, Puerto Rico, and the US Virgin Islands (Appendix 2, Figures 12-13). It was virtually absent from sites in the Florida Keys and southeast Florida visited after 2016 and in the Dry Tortugas at sites visited after 2017 (Appendix 2, Figure 12). The percentage of sites visited with *A. cervicornis* present was more temporally uniform in Puerto Rico and the US Virgin Islands, though still low at <7% of sites in Puerto Rico and <5% of sites in the US Virgin Islands (Appendix 2, Figure 13).

2.3.1.1.5 Habitat or ecosystem conditions (e.g., amount, distribution, and suitability of the habitat or ecosystem):

In a study of *A. cervicornis* colonies transplanted onto a variety of Florida reefs, the most influential drivers of growth, bleaching, and survivorship were abiotic environmental factors, though the impact of specific metrics (temperature, carbonate chemistry, light, etc.) were difficult to resolve (Drury et al. 2017a). Coral genotype also influenced growth rates, bleaching, and mortality though more subtly than environmental factors. Some genotypes appeared to be more generalists that displayed more consistent growth rates across environments, whereas others appeared to be more specialists that thrived only under certain conditions and had low growth rates outside those conditions.

In a survey of 23 restoration sites at six reefs in the Florida Keys, the percent cover of the brown macroalgae of the genus *Dictyota* was found to influence survival of *A. cervicornis* (van Woesik et al. 2018). Survival was highest at sites with <15% *Dictyota* cover, suggesting *Dictyota* spp. negatively influence the growth and survival of *A. cervicornis*.

In a study examining the probability of occurrence of coral species at 985 sites in Florida surveyed from 2011-2015, *A. cervicornis* had one of the smallest areas of suitable habitat (van Woesik et al. 2020b). Suitable habitat was limited to nearshore reefs in Miami-Dade and Broward Counties, the upper and lower Florida Keys, and the Dry Tortugas. The best environmental predictors of presence of *A. cervicornis* were sea surface temperature range (4-5°C difference in daily minimum and maximum temperature) and turbidity (K490 between 0.15-0.25 m^{-1}). Although historically *A. cervicornis* was reported in clear oligotrophic waters, this study found *A. cervicornis* living in nearshore turbid conditions, which may shade corals during high-temperature events.

A study was conducted in the Cayman Islands to evaluate the performance of nursery-raised *A. cervicornis* colonies outplanted to three reef zones of varying depths: back reef (0-3 m), spur and groove (8-15 m), and reef terrace

(>15 m) (Lohr et al. 2017). Wild populations occurred in each zone, but survival of outplanted colonies was lowest in the deep reef terrace. Growth and branching was lowest in the shallow back reef due to high rates of colony breakage, and the authors concluded that the intermediate spur and groove zone was best for *A. cervicornis* restoration efforts. Similarly, a study of 22,635 outplanted *A. cervicornis* colonies in Florida found survival was highest when outplanted to back-reef and fore-reef habitats and at the higher latitudes of the Florida reef tract (van Woesik et al. 2020a).

2.3.1.2 Five-Factor Analysis (threats, conservation measures, and regulatory mechanisms)

2.3.1.2.1 Present or threatened destruction, modification or curtailment of its habitat or range:

Loss of recruitment habitat continues to be a threat to Caribbean corals, including *A. cervicornis*. The presence of algae can inhibit settlement of coral larvae, and in many locations in the Caribbean, there has been a shift from coral dominated to algal dominated reefs partially attributed to the loss of herbivores, including the Caribbean-wide die-off of the long spined sea urchin *Diadema antillarum* and the trophic effects of over-fishing. There is no new information about the magnitude of this threat to *A. cervicornis*.

2.3.1.2.2 Overutilization for commercial, recreational, scientific, or educational purposes:

Although *A. cervicornis* is susceptible to collection and trade, it is a low threat that did not contribute to its status. No new information indicates a change in the magnitude of this threat.

2.3.1.2.3 Disease or predation:

Disease

Acropora cervicornis is highly susceptible to disease, and disease continues to be a large source of mortality. Although disease etiology is still not well understood, disease in *A. cervicornis* is often associated with other stressors. Disease outbreaks have been observed following storm damage and anomalously high water temperature, and several coral predators have been shown to be disease vectors. Disease is often the greatest source of mortality observed in monitoring surveys, and consequently the ability of *A. cervicornis* to recover can depend on the length of time between disease outbreaks. In one study, the rate of tissue loss in *A. cervicornis* was similar between white band disease (0.8 mm/day) and Caribbean ciliate infections (0.7 mm/day) (Verde et al. 2016). Tissue regeneration was 15 times slower than the mortality rates for both diseases.

There have been new studies on the causes and potential vectors for disease. After exposure to disease-causing pathogens in a laboratory study, zooplankton acted as a vector for white band disease affecting *A. cervicornis*

(Certner et al. 2017). Several studies have examined the bacterial profiles of white band diseased colonies, healthy colonies, and/or disease resistant colonies of *A. cervicornis* in an effort to determine a putative pathogen (Certner and Vollmer 2018; Gignoux-Wolfsohn et al. 2017; Gignoux-Wolfsohn et al. 2020; Gignoux-Wolfsohn and Vollmer 2015; Klinges et al. 2020; Rosales et al. 2019; Sweet et al. 2014), but there is still no clear causative agent.

Several studies have examined disease resistance, potential disease treatment, or mitigation strategies. In a study examining disease dynamics and mitigation strategies in the Florida Keys, there was no difference between wild and restored colonies in disease quality, quantity, dynamics, or health management strategies (Miller et al. 2014). Neither excising apparently healthy branches from diseased colonies nor placing a band of epoxy over the disease margin showed significant benefit. In another study examining four antibiotic treatments, two antibiotics, ampicillin and paromomycin, stopped white band disease completely (Sweet et al. 2014). A field test of 31 genotypes of *A. cervicornis* showed genotypic variation in both disease susceptibility (percent of exposed fragments that displayed tissue loss) and the rate of tissue loss of fragments with elicited lesions (Miller et al. 2019).

Predation

Acropora cervicornis is highly susceptible to predation. Predation continues to be a chronic stressor that can affect colony growth and survival through removal of tissue. In a study of survival of *A. cervicornis* colonies outplanted in the Dominican Republic for restoration, the most common cause of mortality both in the coral nursery and in outplanted colonies was predation by the fireworm *Hermodice carunculata* (Calle-Trivino et al. 2020). In a study in Florida, impacts from damselfish were more prevalent (22% of colonies) than prevalence of other stressors such as competitive overgrowth, other predators, or disease (Schopmeyer and Lirman 2015). Impacts from damselfish caused more tissue mortality (35%) than the other stressors, and coral growth rates of colonies with damselfish lawns were almost half as much as those without. However, the presence of damselfish decreased predation by other corallivores such as *Coralliophila* snails and *Hermodice* fireworms (Schopmeyer and Lirman 2015).

In a study examining the susceptibility of *A. cervicornis* tissue condition to predation by the snail *Coralliophila abbreviata*, snails preferred fragments that were diseased or mechanically damaged over healthy fragments (Bright et al. 2015). Further, snails always chose coral fragments undergoing predation by another snail but did not show preference for undisturbed fragments with non-feeding snails. This study demonstrated that there are potential feedbacks that may exacerbate damage from predation in coral populations affected by other types of disturbance such as disease (Bright et al. 2015).

Another study examined the effect of neighborhood coral composition on snail foraging behavior (Johnston and Miller 2014). The study found that corallivorous snails preferentially preyed upon *A. cervicornis* colonies with other neighboring *A. cervicornis* colonies, followed by *A. cervicornis* colonies with a heterospecific (*Orbicella faveolata* colonies) as neighbors. Additionally, snail abundance after initial colonization was negatively correlated with growth of the focal colony.

In a laboratory study, the presence of the carnivorous snail *Thais deltoidea* resulted in a higher percentage of live tissue in *A. cervicornis* when *Corallophila galea (previously C. abbreviata)*, a corallivorous snail, was present (Delgado and Sharp 2020). Although *C. galea* is not a preferred prey choice of *T. deltoidea*, it did consume *C. galea* and elicited an escape response in the corallivore that resulted in less time feeding on *A. cervicornis* fragments.

2.3.1.2.4 Inadequacy of existing regulatory mechanisms:

The threats related to global climate change, including bleaching from ocean warming, ocean acidification, and increased disease (Maynard et al. 2015), pose the greatest potential extinction risk to corals and in the last review were evaluated with sufficient certainty out to the year 2100. We relied on information in the Intergovernmental Panel on Climate Change (IPCC) Fifth Assessment Report (AR5), Climate Change 2013: The Physical Science Basis (IPCC 2013), commonly referred to as the Working Group I Report (WGI). This report presented four Representative Concentration Pathways (RCPs) to simulate future climate change, and we evaluated extinction risk using RCP8.5 which represented the high emissions pathway we were currently on.

The IPCC is now in its sixth assessment cycle (AR6) and has released the WGI report Climate Change 2021: The Physical Science Basis (IPCC 2021) that addresses the most updated physical understanding of the climate system and climate change. The latest report indicates that greenhouse gases have continued to increase in the atmosphere since the 2011 measurements reported in AR5. Strong warming has been observed since 2012, and 2016–2020 was the hottest five-year period recorded since at least 1850. Global surface temperature was 1.09°C higher in 2011–2020 than in 1850–1900. On the current emissions trajectory (RCP8.5), the onset of annual severe coral bleaching in the Caribbean is predicted to occur in 2040-2043 with some regional variation (van Hooidonk et al. 2015); under RCP4.5, which represents lower emissions mid-century than will occur if pledges made following the 2015 Paris Climate Change Conference (COP21) become reality, annual coral bleaching is predicted to occur 11 years later, thus doing little to give corals more time to adapt and acclimate (van Hooidonk et al. 2016). Therefore, existing regulatory mechanisms have continued to be inadequate to protect against climate change and the threat it poses to corals due to ocean warming, ocean acidification, and related increases in disease.

AR6 considers five greenhouse gas scenarios: very low (SSP1-1.9), low (SSP1-2.6), intermediate (SSP2-4.5), high (SSP3-7.0), and very high (SSP5-8.5). The report indicates that global surface temperature will continue to increase until at least 2050 under all five emission scenarios considered in the report. Crossing the 2°C global warming level in the period 2041–2060 is "very likely" to occur under the very high emissions scenario (SSP5-8.5), "likely" to occur under the high emissions scenario (SSP3-7.0), and "more likely than not" to occur in the intermediate emissions scenario (SSP2-4.5). In the nearer term (2021-2040), the 1.5°C global warming level is "very likely" to be exceeded under the very high GHG emissions scenario (SSP5-8.5), "likely*"* to be exceeded under the intermediate and high emissions scenarios (SSP2-4.5 and SSP3-7.0), "more likely than not*"* to be exceeded under the low emissions scenario (SSP1-2.6) and "more likely than not*"* to be reached under the very low emissions scenario (SSP1-1.9). With additional global warming, there is high confidence that the frequency of marine heatwaves will continue to increase, particularly in the tropical ocean. There is "likely" to be a global increase in marine heatwaves of 2–9 times in 2081–2100 compared to 1995–2014 under the low emissions scenario (SP1-2.6) and 3–15 times under the very high emissions scenario (SSP5-8.5). Thus, projected warming is expected to increase in the future.

2.3.1.2.5 Other natural or manmade factors affecting its continued existence:

Ocean Warming

Acropora cervicornis is highly susceptible to ocean warming, and increased temperature due to climate change continues to be a major threat to *A. cervicornis*. A severe bleaching event was reported in 2014 in Florida where most *A. cervicornis* and nearly all massive coral colonies in Hawks Channel were affected (NOAA Coral Reef Watch 2015). Global bleaching events followed in 2015 and 2016 (NOAA Coral Reef Watch 2016; NOAA Coral Reef Watch 2017). One study predicted that *A. cervicornis* is unlikely to survive past 2035 (Langdon et al. 2018) due to increased thermal stress events. Thermal anomalies and coral bleaching events are expected to continue and worsen until greenhouse gas emissions can be reduced.

Thermal tolerance of *A. cervicornis* varies widely among genotypes. A study of how outplanted *A. cervicornis* colonies responded to a naturally occurring thermal stress event found a three-fold difference in survivorship among genotypes (Ladd et al. 2017). In another study of a naturally occurring thermal stress event in a coral nursery, significant differences in prevalence of bleaching and growth (total linear extension, number of branches, and calcification) were observed among genotypes, and growth rates decreased after bleaching (Lohr and Patterson 2017).

There have been new studies on the effects of temperature on *A. cervicornis*. In a laboratory experiment, *A. cervicornis* experienced significantly reduced larval survivorship and lower realized settlement under elevated temperatures of 30.5-31.5°C (Miller et al. 2020a). In a study examining thermal tolerance (32°C) of 20 *A. cervicornis* genotypes from Florida, 40 genes were consistently different between heat tolerant and heat susceptible colonies and could be potential biomarkers for thermal tolerance (Yetsko et al. 2020).

Studies have also examined the effect of temperature in combination with other stressors. A study examining the interaction of high water temperature and white band disease in *A. cervicornis* found that 27% of the 15 genotypes tested were disease resistant prior to a thermal anomaly (~2°C above historical averages represented by 8 degree heating weeks) that caused bleaching (Muller et al. 2018). After exposure to the high water temperatures, disease resistance was essentially lost in all genotypes tested. The temperature stress created an increased risk in disease-associated mortality, suggesting that genets may rarely maintain or gain disease resistance under high temperatures.

A hindcast study was undertaken to examine the relationship between ocean warming and outbreaks of white band disease (Randall and van Woesik 2015). The study compared eight sea surface temperature metrics, including rates of change and thermal anomalies, with records of white band disease from 437 sites surveyed across the Caribbean from 1997 to 2004. The model results indicated that decades-long climate-driven changes in sea surface temperature, increases in thermal minima, and the breach of thermal maxima have all played significant roles in the spread of white band disease. The authors concluded that white band disease has been strongly related to thermal stresses associated with climate change.

Acidification

Results of recent studies examining the effects of ocean acidification on *A. cervicornis* have been mixed. In one study, microfragments of *A. cervicornis* maintained photosynthesis, calcification, and linear extension rates under elevated pCO_2 (~1000 µatm) exposure for 28 days (Bedwell-Ivers et al. 2017). In another, *A. cervicornis* colonies exposed to elevated temperature (30°C), enriched pCO_2 (800 ppm), or both (30°C/800 ppm) for 8 weeks experienced significant decreases in growth as compared to controls (26°C/390 ppm) (Langdon et al. 2018). However, when these corals were fed, they were able to maintain ambient growth rates at both elevated temperature and elevated CO_2 (Langdon et al. 2018). Another experiment exposing *A. cervicornis* to elevated temperature (32°C), elevated CO_2 (800 ppm), or both found that all colonies exposed to elevated temperature died within 25 days while *A. cervicornis* exposed to enriched CO_2 did not experience a significant decrease in growth (Langdon et al. 2018). An experiment that exposed *A. cervicornis* to variable levels of pH (7.80 ± 0.20, 7.80 ± 0.10, 7.80 ± 0.00, 8.05 ± 0.10, and

8.05 ± 0.00) found that those that experienced variable contemporary conditions (8.05 ± 0.10) calcified faster than those in current and future static treatment levels (Enochs et al. 2018).

Sedimentation

Acropora cervicornis is susceptible to sedimentation and turbidity. There is no new species-specific information to indicate changes in the magnitude of this threat.

Nutrients

Acropora cervicornis is susceptible to nutrient enrichment. There is no new species-specific information to indicate changes in the magnitude of this threat.

Conservation Measures

Restoration of *A. cervicornis* using colonies raised in coral nurseries and outplanted back to the reef is a strategy that has been increasing throughout the Caribbean, both in the number of nurseries and the number of outplanted corals. In the United States alone, there were more than 150,000 *A. cervicornis* colonies outplanted between 2014 and 2018 (Moulding et al. 2020). Outplanted corals generally have high survival (60-90%) during the first year or two after outplanting (Calle-Trivino et al. 2020; Mercado-Molina et al. 2015a; Mercado-Molina et al. 2015b; Schopmeyer et al. 2017). However, survival on longer time scales is much lower. In a study of 2,419 outplanted *A. cervicornis* colonies, survivorship was initially high but decreased after two years, ranging from 4-89% for 7 cohorts monitored at least 5 years (Ware et al. 2020). Models to estimate survival beyond the monitoring duration estimated a range of 0 to greater than 35% after 5 years and 0-10% after 7 years. The model predicted that approximately one third of colonies surviving 4 years would be ≥ 50 cm in maximum diameter, and about 15% would reach greater than 100 cm maximum colony diameter. The authors concluded that outplanting protects against local extinction and helps maintain genetic diversity in the wild (Ware et al. 2020). Similarly, in a resurvey of sites in the Florida Keys 10 years after the initial survey, a dramatic increase in density (>13 times the initial density) occurred at sites that had received outplanted colonies; sites that had not received outplants suffered a decline of 0.4-0.7 times the initial density, indicating population enhancement activities confer a substantial reef-scale benefit (Miller et al. 2016a).

There has been debate in the scientific community about the utility of restoration if threats to the species remain unabated. One beneficial outcome is that nursery-reared corals have been found to be reproductively active (Calle-Triviño et al. 2018) and may contribute to sexual reproduction and persistence of the species. Another supportive argument is that restoring corals may enhance ecosystem function. The results of a study of four restoration sites (500-2,300 corals outplanted) in the Florida Keys were a 4-fold increase in coral cover and higher herbivory at some of the sites; however, restoration over the three year period was not enough to facilitate the positive feedbacks that can help reinforce coral success (Ladd et al. 2019). Therefore, longer time frames may be needed to realize any potential ecosystem benefits of coral restoration.

There have been a number of publications studying outplanting methods and optimization. One study of techniques found that outplanting colonies by directly transplanting and manually attaching them to the reef was more successful than not attaching them and more cost effective than having a short grow-out period in a coral nursery (Forrester et al. 2019). Another study found colonies attached with a nail and cable tie had higher survival than those attached with epoxy or attached to a small cement disk (Goergen and Gilliam 2018). Outplanting at lower density generally resulted in higher survival (Goergen and Gilliam 2018; Ladd et al. 2016) and better growth (Griffin et al. 2015; Ladd et al. 2016). Larger colonies survived better than smaller colonies (Goergen and Gilliam 2018; Mercado-Molina et al. 2015b). A colony size of 15 cm total linear length has been suggested as the minimum outplant size (Goergen and Gilliam 2018; van Woesik et al. 2020b).

2.3.1.3 Synthesis

At the time of the last status review, *A. cervicornis* was determined to be threatened. Factors that contributed to the threatened status include reduced abundance and decreasing presence on reefs as well as its susceptibility to local and global threats that are expected to increase in the future. *Acropora cervicornis* abundance, distribution, and life history strategy of fast growth rates and asexual reproduction through fragmentation allow the species to persist despite extremely low recruitment and moderate the species' vulnerability to extinction. It was expected that this buffering capacity would decrease with declining populations as threats were predicted to increase into the future. *Acropora cervicornis* was not considered to be endangered at the time of the last review because its absolute abundance was still high with small pockets of robust remnant populations, because the percent cover and proportion of reefs in the Caribbean where *A. cervicornis* was dominant had stabilized, because there was evidence of limited population expansion in some portions of its range under some circumstances, and because exposure to threats was moderated by its inhabitation of multiple habitats across a moderate depth range that would experience highly variable thermal regimes at local and regional scales.

Since the last status review in 2014, there have been additional studies on the life history of *A. cervicornis*. There is evidence showing poor survival and growth of naturally occurring fragments but high growth and survival of intentionally produced fragments that are grown in nurseries for propagation efforts. There appear to be genotypic differences in growth and calcification rates that may not be consistent in different environments such as nurseries and natural reefs.

Studies since the last review provide new information on population abundance, trends, and distribution. New reports indicate extensive thickets and cover of *A. cervicornis* in Coral Gardens, Belize and confirm relatively high abundance in southeast Florida. However, *A. cervicornis* still exists mostly as smaller, scattered colonies throughout its range, and surveys indicate fewer sites with *A. cervicornis* present in Florida, Cuba, and Colombia. Genetic and genotypic variation appear to remain high in most locations, though many populations maintain themselves through asexual fragmentation rather than new sexual recruitment. Population trends are stable or declining with variations on both temporal and spatial scales. In periods of stable environmental conditions, some populations are able to grow and recover from losses due to disturbances such as storms and disease events. However, with increasing frequency of these disturbances observed and expected in the future due to climate change, the ability of these populations to maintain themselves will likely decline. Conservation efforts such as propagating corals in nurseries to use for population enhancement activities appear to be effective at increasing coral cover and keeping population growth positive with continuous input. These efforts are important at local scales to prevent local extirpation, but they likely will not be enough for species recovery without the abatement of global threats.

Acropora cervicornis was determined to be highly susceptible to ocean warming. Since the last status review, there have been additional bleaching events in which *A. cervicornis* was observed to bleach, and a new study has found negative effects of increased temperature on *A. cervicornis* larval survival and settlement. There appears to be some genotypic variation in thermal tolerance with genotypic differences observed in bleaching prevalence, survival, and growth, and potential biomarkers of thermal tolerance have been identified. A hindcast study found that ocean warming related to climate change may have played a role in the spread of white band disease in *A. cervicornis*. All the new information supports the conclusion that *A. cervicornis* is highly susceptible to ocean warming.

Acropora cervicornis was determined to be highly susceptible to disease at the listing and last status review. New studies since the last status review have attempted to determine causes of white band disease and identify potential treatments. Bacteria appear to play a role in white band disease, though there is still no consensus on the causative agent. However, disease progression has been stopped with certain antibiotics. There appears to be some genotypic differences in both the susceptibility and rate of progression of white band disease, but disease is still often the greatest source of mortality observed in monitoring surveys. Additionally, there is evidence that disease resistance may be reduced under temperature stress. Therefore, *A. cervicornis* remains highly susceptible to disease.

In the last status review, *A. cervicornis* was identified as highly susceptible to ocean acidification. New studies since the review have shown mixed results. Some studies have shown a reduction in *A. cervicornis* growth under elevated pCO_2 while others have not. One study that showed reduced growth under elevated pCO_2 found that the colonies could maintain normal growth under elevated pCO_2 if they were fed. Finally, a study found that *A. cervicornis* that experienced variable contemporary pH conditions calcified faster than those in static pH conditions representing both current and future predicted levels. Based on the new information, we conclude that although there may be circumstances that reduce the effects of ocean acidification on *A. cervicornis*, the species is still highly susceptible.

Acropora cervicornis is highly susceptible to predation. New studies since the last status review confirm that predation is a chronic stressor that can reduce growth and survival through the removal of tissue. A new study showed that corallivorous snails preferentially prey on *A. cervicornis* colonies in close proximity to other *A. cervicornis* colonies and that they preferentially fed on tissue damaged through feeding by other snails or disease. Thus, there may be potential feedbacks that can exacerbate the effects of predation on populations affected by other disturbances. These new studies confirm that *A. cervicornis* is highly susceptible to disease.

At the time of the last status review, *A. cervicornis* was determined to be highly susceptible to sedimentation and nutrients and susceptible to trophic effects of fishing and anthropogenic and natural abrasion and breakage. There has not been any new species-specific information related to these threats.

In summary, although populations of *A. cervicornis* and the buffering capacity of its life history strategy continue to decrease, the species still inhabits its historical range and has small pockets of remnant abundant populations. The proportion of reefs where *A. cervicornis* is present appears to be decreasing in some areas and appears to be more stable, though low, in others. The susceptibility of *A. cervicornis* to threats identified at the time of listing has not changed. Population enhancement has increased in popularity and scope and may aid in conservation of the species on local scales. Based on all these factors, *A. cervicornis* continues to be at risk of becoming an endangered species in the foreseeable future but does not appear to be currently at risk of extinction. Thus, no change in status is recommended at this time.

2.3.2 ACROPORA PALMATA

2.3.2.1 Biology and Habitat

2.3.2.1.1 New information on the species' biology and life history:

There have been new publications on sexual reproduction in *A. palmata*. A study examining reproductive compatibility found that the overall average fertilization rate was 58% across 10 interspecific crosses of *A. palmata* (Miller et al. 2018). The authors interpreted the variable fertilization rate as an indication of both parental incompatibility and low-quality gametes. In the Florida Keys, a low genet population of *A. palmata* failed to spawn within the predicted window 3 out of the 8 years of observation and had negligible spawning in a fourth year (Miller et al. 2016b). Some genets had significantly greater odds of spawning overall, and certain genets predictably spawned on the earlier side of the window while others spawned on the later side. These studies support the belief that depensatory processes are affecting the species.

There have also been new studies on *A. palmata* larval duration and settlement. One study examining larval duration found that larval metamorphosis without settlement cues began on day 10-11 after spawning and that there was high larval mortality up to 4-5 days after spawning (Miller et al. 2020a). The maximum larval longevity was 70 days. In the presence of settlement cues, onset of settlement occurred earlier at 3-4 days post spawning with rates increasing at 6-8 days; settlement peaked at days 8-15. The study also found significantly reduced survivorship and lower realized settlement under elevated temperatures (Miller et al. 2020a). In a study of *A. palmata* post-settlement survival, survivorship of colonies settled in the lab and placed out on the reef for 6-9 weeks varied from 12% to 49% over the observed duration (Miller 2014).

In a study of the effects of partial mortality on *A. palmata*, there were no differences in growth rate or percent fertilization between colonies with partial mortality and those without, though growth over the lesions did not occur during the 4-month period of observation (Piñón-González and Banaszak 2018). There were differences in lipid levels at the edge of lesions and in egg volume. The authors concluded that partial mortality has a negative effect on the energy budget of *A. palmata* and reduces the quality of eggs (Piñón-González and Banaszak 2018).

2.3.2.1.2 Abundance, population trends (e.g. increasing, decreasing, stable), demographic features (e.g., age structure, sex ratio, family size, birth rate, age at mortality, mortality rate, etc.), or demographic trends:

There have been several studies documenting the abundance or presence of *A. palmata* in the Caribbean. A survey of Pedro Bank, Jamaica had several shallow locations with small, but recovering *A. palmata* stands (Bruckner et al. 2014). Sparse *A. palmata* colonies were found on almost all coral reefs surveyed around Guadeloupe, but dense populations were rarely observed (Japaud et al. 2015). A survey in 2012 at Cayo Sombrero in Venezuela found that the mean density of live *A. palmata* stands (n=19) was 0.3 colonies m^{-2}, and size ranged between 1,800 and 3,600 cm^2 (Martínez et al. 2014). Cover of live *A. palmata* was 60% (Martínez et al. 2014). A study of 106 sites surveyed in 2014 in Los Roques, Venezuela found that *A. palmata* only occupied 15% of the sites surveyed (Croquer et al. 2016). Large standing dead colonies were common throughout the study sites. The majority of living colonies were large adults (~2 m in height), but 45% of surviving colonies exhibited partial mortality and degradation of living tissue. Density had decreased at sites that had previously (2007) had high abundance and low disease prevalence. The authors hypothesized the decline since 2007 was a result of two bleaching events that caused an unprecedented decline in overall coral cover in the region (Croquer et al. 2016).

A survey of 41 shallow reef sites around the Cuban archipelago was conducted between 2010 and 2012, constituting more than 50% of the reefs where *A. palmata* is known to occur in Cuba (Caballero-Aragón et al. 2020). Only 27 (of the 41) sites had more than 10 colonies. Density was less than 5 colonies 10 m^{-1} for all but one site; median density was 1 colony 10 m^{-1} (range 0-13 colonies 10 m^{-1}). Diameter ranged from 10 to 600 cm with 70% of the sites having a median diameter of less than 200 cm. Only one site had a median diameter of >240 cm. Mortality was high at many of the sites. Six sites had 100% mortality (standing dead colonies), and six sites had more than 50% of the colonies with 100% mortality. Fifty percent of the sites had more than 50% partial mortality, and eight sites had more than 50% of colonies with less than 25% partial mortality. At three sites, *A. palmata* was dominant (>50%) with respect to the other coral species. The three sites with the best conditions were Faro de Cazones, Cayo Fragoso, and Baracoa. The authors concluded that the low percentage of live coral tissue in most of the sites limits the reproductive potential of the species and thus the resiliency of reef crests (Caballero-Aragón et al. 2020).

Surveys of the forereef zones of the reef crest of Jardines de la Reina National Park in Cuba (about 55 linear km surveyed) in 2017 revealed a total of 6,920 colonies of *A. palmata* (Hernandez-Fernandez et al. 2019). Abundant standing dead colonies of *A. palmata* were observed. There were 106 thickets of *A. palmata,* ranging from 8 to 12 colonies, and 3,473 fragments. White band disease affected 1.3% of *A. palmata* colonies. The maximum diameter of the majority of *A. palmata* colonies (63.5% measured) ranged from 0 to 100 cm with about 44% having a diameter of 50-100 cm (Hernandez-Fernandez et al. 2019).

In a study in Belize using satellite imagery and benthic classification to predict new areas of occurrence of *Acropora*, 9 of 11 predicted areas were confirmed to contain healthy *Acropora* spp. (Busch et al. 2016). The study identified 7.58 ha of reef in the shallow (<7 m depth) reef crest and back-reef area dominated by *Acropora* spp. at Coral Gardens, which is one of the largest populations in the Caribbean Sea. Most visually-assessed sites were dominated by *A. cervicornis*, but *A. palmata* was not uncommon. Ground-truthing revealed that the reef crest areas were dominated by *A. palmata*, but lagoonal areas were strongly dominated by *A. cervicornis* with some *A. palmata,* and the hybrid *A. prolifera*, present. The largest patches were close to 2 ha in size, and the smallest appear as scattered isolated patches of only a few square meters (Busch et al. 2016).

Surveys were conducted between 2007 and 2013 at 24 reefs within the Veracruz Reef System in Mexico. *Acropora palmata* was present at 7 of the 11 sites surveyed in the northern group and all 13 sites in the southern group and tended to occur along the windward side of reefs along the reef edges or crests (Larson et al. 2014). A total of 1,804 colonies were assessed, and density ranged from 0.02 to 0.28 colonies m^{-2}. Average colony size was 58 cm in diameter, and average live tissue was 89%. Prevalence was low for damselfish (5%), snails (2%), fireworms (1%), and disease (3%). At each site 15-68% of the colonies were mature (>1,600 cm^2). Two sites were surveyed more than once, and live tissue area decreased at both sites between the initial and subsequent surveys. One site had a decrease in mean live tissue from 96% in 2011 to 73% in 2013; the other had a decrease from 92% in 2011 to 87% in 2012. Density of colonies increased at both sites between 2011 and 2012 which was likely a result of the passage of two storms (Larson et al. 2014).

Surveys for *A. palmata* were conducted between 2010 and 2012 at 107 shallow (≤10 m) reef sites along the Mesoamerican Reef System (23 in Mexico, 36 in Belize, 47 in Honduras, and 1 in Guatemala). *Acropora palmata* was recorded in only a fifth (21 out of 107) of the sites (10 in Mexico, 7 in Honduras, 4 in Belize, none in Guatemala), and it was patchy and rare in the majority of these sites with average cover of 4% (Rodriguez-Martinez et al. 2014). There were only three sites (La Bandera and Limones in Mexico and Cay Caulker in Belize) where *A. palmata* was present in >50% of the transects and had a median percent cover greater than zero. Only one site (Limones reef) in Mexico had high *A. palmata* abundance and cover of 35%, and more in depth surveys were conducted here. At this site, density was 2 colonies m^{-2}, and the size class distribution was skewed towards smaller (<50 cm diameter) size classes. Approximately 84% of the colonies appeared healthy at this site, and disease prevalence increased with colony size. Predators (snails, fireworms, and damselfish) were only present on 0.3% of colonies, and 72% of the colonies had no partial mortality. By comparison, historical data show *A. palmata* was present at 74% of the 31 sites surveyed in the northern section of the Mesoamerican Reef System (Mexico) in 1985 but only at 48% of the sites in this study (2010-2012). Cover was also lower at 3% in 2010-2012 compared to 8% in 1985 (Rodriguez-Martinez et al. 2014).

There have been some studies of *A. palmata* population trends and demographics. In a study of 10 sites in St. John, US Virgin Islands, conducted between 2004 and 2010, *A. palmata* colony density did not significantly change over the course of the study (Muller et al. 2014). Average density was 0.027 colonies m^{-2} in 2004 and 0.036 colonies m^{-2} in 2010. Two sites showed a temporal shift towards more large-sized colonies (max diameter >50 cm) while 7 sites showed no change in size frequency distribution. White pox disease prevalence averaged 19% in 2004 and 3% in 2010 and was more common on large colonies (Muller et al. 2014). There is evidence of *A. palmata* population growth along 4 km of coastline in St. John, US Virgin Islands between 1990 and 2014 (Edmunds 2014). Approximately 1,055 colonies ha^{-1} were observed in 2014, and many of the colonies were about 15 cm diameter, suggesting they appeared within the last 5 years. Sexual recruitment was still low with only 7 recruits observed in annual surveys from 1994-2014 (Edmunds 2014).

Declines of *A. palmata* in Florida have been steep. In the Florida Keys, density of *A. palmata* in 2014 and 2015 was 0.4-0.7 times less than density in 2005-2007; these declines occurred despite very low levels of coral outplanting at some sites (Miller et al. 2016a). Demographic monitoring of *A. palmata* populations between Carysfort and Molasses Reefs in the upper FL Keys have been ongoing since 2004. No larval recruits settled during the 15 years of study (Williams et al. 2020a). Loss of genotypes has occurred both in years of disturbance and when the population appeared to be stable or increasing (2006-2010), dropping by 64% over the 15 years of study (Williams et al. 2020a). Of the remaining genotypes, half (9 of 18) are incapable of spawning due to low amounts of surviving tissue. The authors conclude that *A. palmata* is already functionally extinct in the studied populations and may experience local extirpation within 6-12 years if the rate of decline is presumed to be constant. However, the rate of decline has accelerated since 2014, indicating extirpation may occur sooner (Williams et al. 2020a; Appendix 2, Figure 40). These patterns are similar to those seen in demographic surveys in the lower Florida Keys and in Biscayne National Park north of the upper Keys sites (Williams et al. 2020a). Of the sites surveyed in the lower Keys, *A. palmata* has been extirpated at 2 sites and remains as only 2 colonies at one site. Remaining plots had catastrophic declines after a hurricane, with 3 sites having minimal recovery and one with continuing decline. There were 73 sites with *A. palmata* in the Florida Keys identified between 2003 and 2018; subsequent visits indicate potentially 42-67% of inferred genotypes at these sites (based on distance between sites) have been lost. About 120 genotypes are being propagated in coral nurseries and outplanted to multiple sites. There are no known remaining patches that have adequate numbers of synchronously spawning genets to produced viable larvae without intervention. To reach the range-wide genotypic diversity in the *Acropora* Recovery Plan (0.5), more genets will be needed than are currently available in Florida, and it will likely take novel approaches in larval rearing and nursery propagation to produce them (Williams et al. 2020a).

Unpublished CREMP data from permanent monitoring stations in the Florida Keys show a decrease in mean percent cover, live tissue area, and density of *A. palmata* between 2014 and 2019 (Appendix 2, Figures 25, 27, and 29). During this time, one monotypic/special habitat site was monitored in the Dry Tortugas and showed more variable percent cover and live tissue area between 2014 and 2019 (Appendix 2, Figures 26 and 28). However, values in 2019 were lower than in 2014. In contrast, density at this site was higher in 2019 than in 2014 (Appendix 2, Figure 30).

In surveys of randomly chosen monitoring sites (different sites visited each year), unpublished NCRMP data show the proportion of sites where *A. palmata* was present ranged from about 2% to 7% in the US Virgin Islands and about 2% to 4% in Puerto Rico between 2014 and 2019 (Appendix 2, Figure 34). The percentage of sites where *A. palmata* was present was 0% to 2% in Florida between 2014 and 2020 with all sites containing *A. palmata* occurring in the Florida Keys (Appendix 2, Figure 34). Mean maximum colony diameter ranged from approximately 30-50 cm in St. Croix, 30-75 cm in St. Thomas/St. John, and 15-50 cm in Puerto Rico (Appendix 2, Figure 35). Mean partial colony mortality between 2014 and 2019 ranged from 0-35% in Puerto Rico and 5-30% in the US Virgin Islands (Appendix 2, Figure 35).

2.3.2.1.3 Genetics, genetic variation, or trends in genetic variation (e.g., loss of genetic variation, genetic drift, inbreeding, etc.):

There have been several studies of genetic or genotypic diversity of *A. palmata*. On a unique reef with dense populations of both *A. palmata* and *A. cervicornis*, Caye-à-Dupon in Guadeloupe, all *A. palmata* colonies in a 30 m radius circular plot were sampled for genetic analysis in December 2011. Genotypic richness was 0.125 (10 genotypes out of 80 samples), indicating that the maintenance of *A. palmata* populations at this site is mostly asexual, and that sexual recruitment on this reef is limited (Japaud et al. 2015). A previous study of Guadeloupean *A. palmata* populations (Mège et al. 2014) showed a much higher genotypic richness (0.96) but used a non-random, opportunistic sampling design to avoid over-representation of clones for the benefit of genetic structure analyses (Japaud et al. 2015).

Between 2011 and 2015, *A. palmata* colonies were sampled at 36 sites from 11 islands in the Lesser Antilles, from St. Martin and St. Barthélemy in the north to the islands of St. Vincent and the Grenadines in the south (across ~600 km), to estimate the genotypic diversity and to assess population genetic structure and connectivity. Out of the 1,042 samples collected, 726 unique genotypes were identified (Japaud et al. 2019). Genotypic diversity ranged from nearly 0 to 1 depending on the site, and average genotypic diversity was 0.75. Average genotypic diversity per island ranged from 0.4 to 1. Sites were categorized as asexual (2 sites), mostly asexual (4 sites), mostly sexual (14 sites), and sexual (15 sites). Per island, the number of genotypes ranged from 30 in Saint Lucia (n=60 samples) to 256 in Guadeloupe (n=395 samples).

Genetic differentiation between islands was generally higher than within islands. The study found that gene flow was oriented along a north-south axis with increasing genetic divergence related to increasing geographic distance between islands. The maximum gene dispersal distance in the Lesser Antilles was estimated as 1 km (Japaud et al. 2019).

A study examining the genetic structure of *A. palmata* from locations in Puerto Rico, Curaçao, the Bahamas, and Guadeloupe found that 75% of the samples (309 out of 412 samples) were unique genotypes and that genetic diversity among genets was high and consistent across locations (Mège et al. 2014). It also found that the genetic divide between the western and eastern populations was likely to the east of Puerto Rico rather than around the Mona passage as previously found (Mège et al. 2014).

Acropora palmata population structure and genetic diversity were assessed at the regional spatial scale of the Mesoamerican Barrier Reef System and at a larger Caribbean-wide spatial scale (Porto-Hannes et al. 2015). The study found high genetic diversity, low clonality, and low population structure among populations of the Mesoamerican reef system. Genotypic diversity of *A. palmata* ranged from 0.65 to 0.98 and on average was 0.87. The isolation by distance model explained genetic structure of *A. palmata* with significant correlation between genetic distance and geographic distance (Porto-Hannes et al. 2015).

Three reef sites (Manatee Channel, Coral Gardens, and Rocky Point) offshore of Ambergris Caye in Belize with abundant *A. cervicornis*, *A. palmata*, and hybrid *Acropora* populations were studied (Irwin et al. 2017). *Acropora cervicornis* and *A. palmata* at Manatee Channel showed the highest genotypic diversity and evenness among locations, indicating that a substantial proportion of local recruitment was via sexual reproduction. Coral Gardens was characterized by low genotypic diversity across all three taxa, indicating a high degree of asexual recruitment. When samples were pooled across all three sites, both diversity and evenness metrics were relatively low and indicated predominantly asexual recruitment. Overall, *A. palmata* showed the highest genotypic diversity, evenness, and richness. The study suggested that while Coral Gardens may be the largest extant acroporid site in the Caribbean (Busch et al. 2016), this site may not make significant contributions towards downstream sexual recruitment.

A genome-wide study of *A. palmata* found that allelic richness of microsatellite loci remains high despite recent population declines and the documented loss of alleles in Florida (Devlin-Durante and Baums 2017). *Acropora palmata* was found to associate predominantly with one species of zooxanthellae (*Symbiodinium 'fitti'*), and samples across *A. palmata*'s range were found to be dominated by this single symbiont genotype (or strain)

(Baums et al. 2014). Gene flow among *A. palmata* was an order of magnitude greater than among populations of the symbiont (Baums et al. 2014).

There have been studies that have used somatic mutations to estimate the age of genets of *A. palmata*. Age of genets was estimated based on rates of mutation calculated in two ways: from colony growth rates (maximum mutation rate) and from the appearance of *A. palmata* in the geologic record in cores taken from Looe Key, Florida (minimum mutation rate) (Devlin-Durante et al. 2016). In a study of somatic mutations of 3,352 samples from 147 *A. palmata* genets collected throughout their range, age of *A. palmata* genets ranged from 30-838 years based on maximum mutation rates and 236-6,500 years based on minimum mutation rates (Devlin-Durante et al. 2016). The ages of 3 *A. palmata* genets offshore of Ambergris Caye in Belize were estimated at a minimum of 187–561 years and a maximum of 1397-4191 years (Irwin et al. 2017). At one site (Manatee Channel), no somatic mutations were observed at the loci amplified for any *A. cervicornis*, *A. palmata*, or hybrid genets; the authors concluded these genets lacked somatic mutations because they were of recent origin. The data suggest that both new (minimal somatic mutations) and veteran genets (minimum ages 187–561 years) co-exist at these sites and that veteran Belize acroporids pre-date the widespread Caribbean collapse of acroporids in the 1980s (Irwin et al. 2017).

There were several studies on genotypic variation of *A. palmata*. In 12 genotypes exposed to disease in the field, there was variation in disease susceptibility (percent of exposed fragments that experienced tissue loss) and in the rate of tissue loss in *A. palmata* fragments that developed lesions (Miller et al. 2019). Phenotypic variation in bleaching within genets was observed during bleaching events in 2014 and 2015 caused by high water temperatures (Durante et al. 2019). It was not due to differences in the symbiont because they typically have only one strain of *Symbiodinium 'fitti.'* Long-term micro-environmental differences may have led to changes in the way the ramets methylated their genomes that contributed to the differential bleaching responses (Durante et al. 2019). In a study of gene expression associated with bleaching of *A. palmata*, the expression level of 38 key proteins differed between bleached and unbleached colonies (Ricaurte et al. 2016). These results suggest that there was a differential protein expression response in bleached colonies (Ricaurte et al. 2016).

2.3.2.1.4 Spatial distribution, trends in spatial distribution (e.g. increasingly fragmented, increased numbers of corridors, etc.), or historic range (e.g. corrections to the historical range, change in distribution of the species' within its historic range, etc.):

There have been several surveys targeting the presence and distribution of *A. palmata*. Around Guadeloupe, sparse *A. palmata* colonies were found on almost all coral reefs surveyed, but dense populations were rarely observed (Japaud et al. 2015). In a survey of 52 stations in St. Croix in 2007 and 52 stations in St. Thomas and St. John in 2009, *A. palmata* was observed in 15% of stations in St. Croix and 10% in St. Thomas and St. John (Fisher et al. 2014). In Cuba, a survey was conducted across 199 reef sites (reef crests and fore reefs) within 12 localities (separation of localities was 100 - 1000 km). The majority of reef crests had deteriorated with *A. palmata* dominant in only 5 out of 36 reef crests surveyed; many reef crests had old standing dead colonies (Caballero Aragón et al. 2019).

In the continental Caribbean and insular area of San Andres, Colombia, surveys of *A. palmata* were conducted between 2016 and 2018 at seven locations containing potential *Acropora* habitat along a latitudinal gradient. Surveys were conducted in 53 shallow reefs, and 1,292 colonies of *A. palmata* were measured (García-Urueña and Garzón-Machado 2020). About 26% of the colonies in the Rosario Islands and in Tayrona National Natural Park had disease, and fish predation occurred in 7% to 34% of colonies. At the sites, the percentage of healthy colonies ranged from 31% to 79%. The largest patch-type formations of *A. palmata* were located in Tayrona National Natural Park, and small isolated patches were observed in Isla Arena, the Urabá Gulf, Isla Fuerte, and the San Bernardo Islands. The rest of the study area was mainly dominated by scattered colonies. In Tayrona National Natural Park it appears that *A. palmata* cover had increased compared with reported cover in 2004 (22% versus 10% in 2004). However, in Isla Arena, cover had decreased from 76% in 1998 to 18% between 2016 and 2018 in the current study, and the species had almost disappeared from Isla Grande reef in the Rosario Islands where the main formation previously appeared (García-Urueña and Garzón-Machado 2020).

2.3.2.1.5 Habitat or ecosystem conditions (e.g., amount, distribution, and suitability of the habitat or ecosystem):

There have been new studies examining settlement inducers, including crustose coralline algae and bacterial films, for *A. palmata* larvae (Ritson-Williams et al. 2016; Ritson-Williams et al. 2020; Ritson-Williams et al. 2014; Sneed et al. 2014). In a study of ten species of red algae, including eight species of crustose coralline algae, several species induced settlement of *A. palmata* larvae, but the ones that induced the highest settlement and metamorphosis of *A. palmata* larvae tended to be rare on Belizean reefs and primarily found in low-light environments (Ritson-Williams et al. 2014).

A study in Akumal, Mexico found that *A. palmata* colonies were able to resheet, or grow over, standing dead coral skeletons (Mudge et al. 2019). A survey of 12 spur and groove reef sites found that both *Diadema* urchins and parrotfish populations were positively associated with increasing *A. palmata* presence and cover and lower macroalgal cover and may facilitate resheeting. Out of 85 colonies or patches measured, 60 had live area index greater than 1600 cm^2 and were considered mature. Average percent cover ranged from 0-6.5% (Mudge et al. 2019).

In a study to gauge the potential for *A. palmata* restoration in the Florida Keys, fragments from 5 genets from the upper Keys were moved to five sites in the Dry Tortugas (Kuffner et al. 2020). All fragments transplanted to the Dry Tortugas survived and calcified about 85% faster than the fewer surviving fragments transplanted in the upper Florida Keys, suggesting that the Dry Tortugas could be a prime location for re-establishing *A. palmata* (Kuffner et al. 2020).

2.3.2.2 Five-Factor Analysis (threats, conservation measures, and regulatory mechanisms)

2.3.2.2.1 Present or threatened destruction, modification or curtailment of its habitat or range:

Loss of recruitment habitat continues to be a threat to Caribbean corals, including *A. palmata*. The presence of algae can inhibit settlement of coral larvae, and in many locations in the Caribbean, there has been a shift from coral dominated to algal dominated reefs partially attributed to the loss of herbivores, including the Caribbean-wide die-off of the long spined sea urchin *D. antillarum* and the trophic effects of over-fishing. There is no new information about the magnitude of this threat to *A. palmata*.

2.3.2.2.2 Overutilization for commercial, recreational, scientific, or educational purposes:

Although *A. palmata* is susceptible to collection and trade, it is a low threat that did not contribute to its status. No new information indicates a change in the magnitude of this threat.

2.3.2.2.3 Disease or predation:

Disease

There have been new studies examining the causes of disease in *A. palmata*. In a study using 16S rRNA gene high-throughput sequencing on *A. palmata* inoculated with disease, a core bacteria member from the order Sphingomonadaceae was identified as a putative coral pathogen, and a bacterium from the order Myxococcales was associated with corals that showed disease resistant phenotypes (Rosales et al. 2019). Another study examined the association of *Vibrio* bacteria with the occurrence of white pox disease in *A. palmata* at Looe Key Reef in the Florida Keys between 2012 and 2014. *Vibrio* concentration was greater in diseased corals than in apparently healthy colonies, and *Vibrio* abundance relative to total bacteria was 4 times higher in diseased lesions than in samples taken from adjacent apparently healthy regions of diseased colonies (Kemp et al. 2018). The authors suggested that *Vibrio* spp. may be part of a nonspecific bacterial bloom rather than a primary pathogen.

Another study examined photographs of diseased *A. palmata* colonies from 1994 to 2014 at eight reefs in the Florida Keys. While white pox prevalence

(0-71%) over time was comparable for the duration of the 20 year study, white pox severity (amount of colony surface area affected) and whole colony mortality were high in outbreaks occurring between 1994 and 2004 and low in outbreaks occurring between 2008 and 2014 (Sutherland et al. 2016). The authors suggest that changes in pathogens, host, and/or environment after the disease state complicate disease etiology studies. The finding that total colony mortality from white pox was less common in more recent years than in the past was confirmed in another study that surveyed 6 reefs in the Florida Keys between 2011 and 2013. White pox disease was observed at 4 of the 6 sites and on 8-40% of the colonies surveyed, but unlike prior outbreaks, no whole-colony death was observed (Joyner et al. 2015).

There were other studies that examined the environmental conditions associated with *A. palmata* disease. A study in Tres Palmas Marine Reserve in Puerto Rico found a relationship between fecal contaminants from septic tanks and condition of *A. palmata* colonies (Norat-Ramírez et al. 2019). A modeling study suggested that decades-long climate-driven changes in sea surface temperature, increases in thermal minima, and the breach of thermal maxima have all played significant roles in the spread of white-band disease in *Acropora* and concluded that white-band disease has been strongly coupled with thermal stresses associated with climate change (Randall and van Woesik 2015). In a study of the covariates that influence the presence of white pox disease in *A. palmata*, colony size, genetic susceptibility, and high water temperatures were the primary tested variables that were positively associated with disease presence (Muller and van Woesik 2014). Because disease presence was not associated with distance from previously infected colonies or colony location, the authors concluded that white pox disease was most likely a result of high water temperature that selectively compromised the oldest colonies and most susceptible genotypes.

Predation

New research was published on the effects of predation on *A. palmata*. Monthly surveys were conducted for a year following a series of large swells in March 2008 that caused colony fragmentation of 30-93% of *A. palmata* colonies at 3 sites in St. Thomas and St. John, US Virgin Islands. *C. abbreviata*, a corallivorous snail, was 46% more abundant on damaged than undamaged colonies (Bright et al. 2016). In a long term study in the Florida Keys, predation by corallivorous snails accounted for one quarter of the tissue lost on *A. palmata* in monitoring plots over 7 years (Williams et al. 2014). Removal of all *C. abbreviata* on *A. palmata* colonies and on all coral species within monitoring plots both reduced prevalence of feeding scars and snail abundance, but there was no significant difference between removal methods (on all coral species versus only *A. palmata* colonies). Snail recolonization to baseline abundance was estimated to be 3.7 years, and recolonization rate was correlated with baseline snail abundance (Williams et al. 2014).

2.3.2.2.4 Inadequacy of existing regulatory mechanisms:

The threats related to global climate change, including bleaching from ocean warming, ocean acidification, and increased disease (Maynard et al. 2015), pose the greatest potential extinction risk to corals and in the last review were evaluated with sufficient certainty out to the year 2100. We relied on information in the Intergovernmental Panel on Climate Change (IPCC) Fifth Assessment Report (AR5), Climate Change 2013: The Physical Science Basis (IPCC 2013), commonly referred to as the Working Group I Report (WGI). This report presented four Representative Concentration Pathways (RCPs) to simulate future climate change, and we evaluated extinction risk using RCP8.5 which represented the high emissions pathway we were currently on.

The IPCC is now in its sixth assessment cycle (AR6) and has released the WGI report Climate Change 2021: The Physical Science Basis (IPCC 2021) that addresses the most updated physical understanding of the climate system and climate change. The latest report indicates that greenhouse gases have continued to increase in the atmosphere since the 2011 measurements reported in AR5. Strong warming has been observed since 2012, and 2016–2020 was the hottest five-year period recorded since at least 1850. Global surface temperature was 1.09°C higher in 2011–2020 than in 1850–1900. On the current emissions trajectory (RCP8.5), the onset of annual severe coral bleaching in the Caribbean is predicted to occur in 2040-2043 with some regional variation (van Hooidonk et al. 2015); under RCP4.5, which represents lower emissions mid-century than will occur if pledges made following the 2015 Paris Climate Change Conference (COP21) become reality, annual coral bleaching is predicted to occur 11 years later, thus doing little to give corals more time to adapt and acclimate (van Hooidonk et al. 2016). Therefore, existing regulatory mechanisms have continued to be inadequate to protect against climate change and the threat it poses to corals due to ocean warming, ocean acidification, and related increases in disease.

AR6 considers 5 greenhouse gas scenarios: very low (SSP1-1.9), low (SSP1-2.6), intermediate (SSP2-4.5), high (SSP3-7.0), and very high (SSP5-8.5). The report indicates that global surface temperature will continue to increase until at least 2050 under all five emission scenarios considered in the report. Crossing the 2°C global warming level in the period 2041–2060 is “very likely” to occur under the very high emissions scenario (SSP5-8.5), “likely” to occur under the high emissions scenario (SSP3-7.0), and “more likely than not” to occur in the intermediate emissions scenario (SSP2-4.5). In the nearer term (2021-2040), the 1.5°C global warming level is “very likely” to be exceeded under the very high GHG emissions scenario (SSP5-8.5), “likely” to be exceeded under the intermediate and high emissions scenarios (SSP2-4.5 and SSP3-7.0), “more likely than not” to be exceeded under the low emissions scenario (SSP1-2.6) and “more likely than not” to be reached under the very low emissions scenario (SSP1-1.9). With additional global warming, there is high confidence that the frequency of marine heatwaves will continue to increase, particularly in the tropical ocean. There is “likely” to be a global increase in marine heatwaves of 2–9 times in 2081–2100 compared to 1995–2014 under the low emissions scenario (SP1-2.6) and 3–15 times under the very high emissions scenario (SSP5-8.5). Thus, projected warming is expected to increase in the future.

2.3.2.2.5 Other natural or manmade factors affecting its continued existence:

Ocean Warming

There were new studies on the effects of ocean warming on *A. palmata*. A spatial distribution model developed in the US Virgin Islands predicted that under scenarios of elevated temperature and significant wave height expected with climate change, *A. palmata* will occur in only a small portion of its potential habitat and that colonies will shift from larger to smaller size classes (Chen et al. 2020). Another study examined the effects of hydrogen peroxide, which corals produce internally under heat stress, on reproduction of *A. palmata*. It found concentrations of 100 $\mu m\ l^{-1}$ or greater caused a significant reduction in fertilization of gametes, metamorphosis, and larval settlement (Ross et al. 2017). A study examining three bleaching events between 2010 and 2015 in the upper Florida Keys found differences between events. During the mild event in 2011, up to 59% of *A. palmata* colonies bleached, but none suffered complete mortality (Williams et al. 2017). Severe and unprecedented bleaching occurred in 2014 and 2015 with up to 100% of *A. palmata* colonies bleached and a decline of live tissue cover by one third. Increased bleaching prevalence corresponded to maximum daily water temperatures above 31.3°C, but the cumulative number of days with the daily average above 31°C was a better predictor of bleaching response. Surviving colonies that bleached in 2014 did not show any acclimatization to previous exposure to high temperatures and bleached at least as badly in 2015 as they had in 2014 (Williams et al. 2017).

Acidification

Acropora palmata is highly susceptible to ocean acidification. There is no new species-specific information to indicate changes in the magnitude of this threat.

Sedimentation

A new study examined the effects of algal turfs and algal turfs plus sediment on *A. palmata* settlement. It found that the presence of naturally accumulating sediment (1-3 mm) reduces settlement 10-fold for *A. palmata* compared to turf algae alone (Speare et al. 2019). The presence of turf algae (1.8–5.2 mm canopy height) alone did not reduce settlement. This result was corroborated by field surveys in the Florida Keys that showed a strong negative relationship between the abundance of turf algae plus sediment (mean sediment depth of 4.6 mm; range 2-7 mm) and the abundance of juvenile corals (Speare et al. 2019).

Nutrients

A 10-month study examining coral-algal interactions under scenarios of fish-mediated nutrients and fish plus anthropogenic nutrients found that nutrients from fish (nitrogen primarily in the form of ammonium) positively affected *A. palmata* growth (Allgeier et al. 2020). In corals exposed to moderate doses of anthropogenic nutrients (nitrogen primarily in the form of nitrate), a shift in coral-symbiotic algal interactions occurred, and nutrient and carbon flow were dominated by the symbiont. The results show that nutrient and carbon pathways are changed under anthropogenic nutrient additions that could increase susceptibility to other stressors (Allgeier et al. 2020).

Conservation Measures

There have been studies on restoration of *A. palmata* using nursery-raised corals, coral fragments, or sexual recruits. One study examined survival of sexually produced *A. palmata* colonies that had spent different amounts of time in a land-based nursery. In Curacao, colonies outplanted to the reef 2 weeks after settlement had a survival rate of 3% after two and a half years post-transplant versus the 0.5% survival rate of those settlers kept in a land-based nursery for 2.5 years (Chamberland et al. 2015).

Another study examined the growth and survival of naturally occurring fragments (n=832) of *A. palmata* that were transplanted to reefs in the British Virgin Islands for restoration (Forrester et al. 2014). Mortality was highest in the first year after outplanting and varied with the year of transplantation (2005-2011). Survival increased with increasing initial fragment size; fragments with surface area roughly 1000 cm^2 fared much better than ones with 100 cm^2 and 10 cm^2. Fragments typically reached 3000 cm^2 seven years after outplanting, but growth was highly variable and largely independent of initial colony size. Long-term survival of transplanted colonies was roughly comparable with natural colonies, and survival of transplanted fragments was much higher than those left unattached (Forrester et al. 2014).

In an experiment examining the effects of size on performance of a single outplanted *A. palmata* genotype, smaller fragments (average 51 cm^2) produced more live tissue area, experienced less bleaching (events occurred in 2014 and 2015), and had equal survivorship to larger fragments (average 108 cm^2) (Pausch et al. 2018). In the same study, a second experiment using 4 genotypes of *A. palmata* outplanted to two reef types (fore reef and mid-channel patch reef) in the Florida Keys found that survivorship, bleaching severity, and net change in size differed among genotypes. In addition, bleaching was less severe and survivorship was less variable among genotypes outplanted in fore reefs (Pausch et al. 2018).

2.3.2.3 Synthesis

At the time of the last status review, *A. palmata* was determined to be threatened. Factors that contributed to the threatened status include *A. palmata*'s substantially reduced abundance, with models predicting local extirpation at some locations, as well as its susceptibility to local and global threats that are expected to increase in the future. *Acropora palmata* abundance, distribution, and life history strategy of fast growth rates and asexual reproduction through fragmentation allow the species to persist despite extremely low recruitment and were determined to moderate the species' vulnerability to extinction. It was expected that this buffering capacity would decrease with declining populations as threats were predicted to increase into the future. *Acropora palmata* was not considered endangered at the time of the last review because its absolute abundance was still high, because the proportion of sites where *A. palmata* was present and dominant had stabilized, because there was evidence of bleaching resistance in some portions of its range under some circumstances, and because exposure to threats was moderated by its inhabitation of multiple habitats across a moderate depth range that would experience highly variable thermal regimes at local and regional scales.

Studies since the last review in 2014 provide new information on population abundance, trends, and distribution of *A. palmata*. There are some areas where populations are still somewhat abundant, such as Coral Gardens in Belize, Jardines de la Reina National Park in Cuba, Veracruz in Mexico, and St. John in the US Virgin Islands. However, *A. palmata* appears to be continuing to decline in most locations surveyed, such as in Cuba, Venezuela, and Colombia, and particularly in the northernmost portion of its range in Florida where declines since 2014 have been steeper than the previous decade. Most locations surveyed have patchy colonies with many colonies displaying partial mortality. There has been a decline in the number of reefs where *A. palmata* is present and little to no signs of sexual recruitment into the population. Depensatory effects such as genet incompatibility and spawning asynchrony hamper sexual reproduction. Genetic and genotypic diversity on a range-wide scale appear to remain high, though can be low at some local and regional scales.

At the time of the last review, *A. palmata* was considered highly susceptible to disease. There have been some recent studies examining the causative agent of diseases though there is still no consensus. New information since the last review indicates that there is genotypic variation in susceptibility of disease (percentage of colonies that experienced tissue loss) and rate of tissue loss in colonies that developed lesions. In the Florida Keys, there is some new evidence that total colony mortality from white pox disease was less common between 2008 and

2014 than it had been in the decade prior to 2004, even though disease prevalence was comparable between time periods. Finally, both white band disease and white pox disease in *A. palmata* have been strongly coupled with thermal stresses associated with climate change. All the new information supports the conclusion that *A. palmata* is highly susceptible to disease.

The last review indicated that *A. palmata* is highly susceptible to ocean warming which can affect bleaching and mortality, susceptibility to disease, and reproduction. New studies confirm these characterizations. Bleaching response and mortality in the Florida Keys was variable among years of elevated temperatures, but previous bleaching did not confer any bleaching resistance to colonies that bleached and survived in the previous year. Thus, *A. palmata* remains highly susceptible to ocean warming.

Acropora palmata was determined to be highly susceptible to ocean acidification at the time of the last review, and there has been no new species-specific information on the susceptibility of *A. palmata* to this threat.

In the last review, *A. palmata* was considered to have some susceptibility to the trophic effects of fishing due to low recruitment rates. Since the review, new information indicates that increasing *A. palmata* coral presence and cover and lower macroalgal cover were positively associated with *Diadema* urchins and parrotfish populations and that their presence may facilitate resheeting of live tissue over dead skeletons. Thus, new information supports the determination that *A. palmata* has some susceptibility to the trophic effects of fishing.

Acropora palmata is highly susceptible to sediments and nutrients. Information since the last review indicates that the presence of naturally accumulating sediment in turf algae reduces *A. palmata* settlement 10-fold compared to turf algae alone. In addition, the exposure of *A. palmata* to anthropogenic nutrients has a negative effect on coral/algal symbiosis that could increase susceptibility to other stressors. Thus, new information supports the conclusion that *A. palmata* is highly susceptible to sediment and nutrients.

At the time of the last review, *A. palmata* was described as highly susceptible to predation. New information from a long-term monitoring study found that predation accounted for 25% of tissue loss on *A. palmata* colonies in the upper Florida Keys. Additionally, the corallivorous snail *C. abbreviata* was found to preferentially feed on damaged tissue. This new information supports the finding that predation can be a large source of mortality on dwindling and degraded populations and confirms that *A. palmata* is highly susceptible to predation.

In summary, although populations of *A. palmata* and the buffering capacity of its life history strategy continue to decrease, the species still inhabits its historical range and has small pockets of abundant populations. The proportion of reefs where *A. palmata* is present appears to be decreasing in some areas. Genetic and genotypic diversity on a range-wide scale appear to remain high. The susceptibility of *A. palmata* to threats identified at the time of the last review has not changed. Based on all these factors, *A. palmata* continues to be at risk of becoming an endangered species in the foreseeable future but does not appear to be currently at risk of extinction. Thus, no change in status is recommended at this time.

2.3.3 ORBICELLA ANNULARIS

2.3.3.1 Biology and Habitat

2.3.3.1.1 New information on the species' biology and life history:

There have been new studies examining the symbiont diversity in *O. annularis*. A study of 552 colonies of *O. annularis* from 33 populations across its range found that the heat-tolerant algal symbiont *Symbiodinium* D1 was present in low abundances in all but one population, with an average of >30% of corals per site hosting the *Symbiodinium* species (Kennedy et al. 2015). The wide-spread prevalence of this thermally tolerant *Symbiodinium* species in *O. annularis* indicates the potential capacity for corals to temporarily respond to warming events through symbiont shuffling. However, the association of *Symbiodinium* D1 is also linked to reduced growth rate of the coral host, suggesting that it may be unlikely to prevent long-term declines (Kennedy et al. 2015).

A study characterizing and mapping symbiont diversity in *O. annularis* found a northwest-southeast partitioning across the Caribbean in both symbiont diversity and the dominant symbiont taxa, a pattern which was predominantly explained by chronic thermal stress (Kennedy et al. 2016). The study was also able to associate the presence of specific symbiont taxa with environmental conditions such as cooler summers, nutrient loading, and turbidity (Kennedy et al. 2016). A separate study examining *Symbiodinium* species between two sites in St. John, US Virgin Islands found differences in symbiont taxa between sites but not between depths, indicating the potential roles of dissimilar environmental conditions in determining the types of symbionts on the scale of a few kilometers (Pochon et al. 2014).

2.3.3.1.2 Abundance, population trends (e.g. increasing, decreasing, stable), demographic features (e.g., age structure, sex ratio, family size, birth rate, age at mortality, mortality rate, etc.), or demographic trends:

There have been several new publications that describe the abundance and population trends of *O. annularis* in surveys conducted prior to the 2014 listing of the species under the ESA. In surveys conducted between 1999 and 2000 at 11 sites along 400 km of the Mesoamerican Reef System in Mexico, *O. annularis* was among the most dominant species on reefs in the central and southern zones (Rodríguez-Zaragoza and Arias-González 2015). A long-term study of photo quadrats in the US Virgin Islands between 1994 and 2010 showed that there was a reduction from 40% to 28% cover of *O. annularis* over the time period (Edmunds et al. 2014).

In a survey of 52 stations in St. Croix in 2007 and 52 stations in St. Thomas and St. John in 2009, *O. annularis* was observed in 31% of the stations in St. Croix and 65% in St. Thomas and St. John (Fisher et al. 2014). However, it had low relative abundance, making up about 9% of the total colonies. Because colonies were large, *O. annularis* accounted for 36% of the total coral surface area but only ~20% of the live tissue area due to partial colony mortality. Average percent live tissue for *O. annularis* was 15% in St. Croix and 37% in St. Thomas and St. John (Fisher et al. 2014).

Surveys conducted in Cuba indicate *O. annularis* has generally declined in abundance and dominance. Surveys were conducted between 2010 and 2016 at 37 sites (terrace edge habitat, 9-15 m deep) interspersed among the seven coral reef systems. *Orbicella* spp. were uncommon to rare, suggesting substantial losses prior to the surveys, but *Orbicella* spp. were moderately common at Península Ancón and Jardines de la Reina (González-Díaz et al. 2018). A separate survey was conducted across 199 reef sites (reef crests and fore reefs) within 12 localities (separation of localities was 100 - 1000 km) of Cuba. In the surveyed fore-reefs, the previous dominance of *O. annularis* had been replaced by more opportunistic species (Caballero Aragón et al. 2019).

Unpublished monitoring data of permanent monitoring sites show population trends of *O. annularis* since the listing. Live coral tissue area in Florida decreased substantially between 2014 and 2015 and then continued to gradually decline until 2019 (Appendix 2, Figure 59). This declining trend was visible in both southeast Florida and the Florida Keys (Appendix 2, Figure 59) as well as in monospecific/special habitat sites in the Dry Tortugas (Appendix 2, Figure 61). In long-term monitoring sites in the US Virgin Islands, percent cover of *O. annularis* decreased slightly overall between 2015 and 2020 with shallower sites (<20 m) showing declines and sites 21-30 m in depth increasing in cover (Appendix 2, Figure 74).

Density information is available from monitoring programs using permanent and random sites. In permanent sites, the density of *O. annularis* in Florida decreased from approximately 0.04 colonies m^{-2} in 2014 to about 0.02 colonies m^{-2} in 2019 (Appendix 2, Figure 62). This trend was primary influenced by *O. annularis* density in the Florida Keys that decreased from about 0.07 colonies m^{-2} to 0.03 colonies m^{-2} over this period (Appendix 2, Figure 62). Density of *O. annularis* at monotypic/special habitat sites in Florida also decreased between 2014 and 2019, and the trend was primarily driven by sites in the Dry Tortugas (Appendix 2, Figure 64). Unpublished NCRMP monitoring data from random sites stratified by habitat type (different sites visited each year) show that density of *O. annularis* was variable between 2014 and 2019 but ranged between 0.05 and 0.15 colonies m^{-2} in Puerto Rico and the US Virgin Islands (Appendix 2, Figure 66).

Additional unpublished NCRMP data from randomly surveyed sites include colony size and partial mortality. Mean colony size was relatively stable between 2014 and 2019 for the US Virgin Islands, Puerto Rico, and the Florida Keys and ranged between 25 and 50 cm (Appendix 2, Figure 69). Average colony size in the Dry Tortugas was highly variable but was approximately 125 cm in 2018 (Appendix 2, Figure 69). Mean colony partial mortality was between 25% and 50% in Puerto Rico and the US Virgin Islands and highest in the Florida Keys, ranging from 50% to 75% (Appendix 2, Figure 69).

The demographics of *O. annularis* were studied on Tektite Reef in St. John, US Virgin Islands over a 25-year period (1988-2013) divided into 5 year intervals (Edmunds 2015). Bleaching and hurricanes affected the reef during three five-year intervals from 1988 to 2002 though *O. annularis* cover over this period increased from 33% to 49%. It subsequently decreased between 2002 to 2007 to 27% and stabilized at about 28% between 2010 to 2013. Over the 25-year period, colonies greater than 50 cm^2 became rare, and the abundance of colonies $\leq$ 50 cm^2 increased from 58% at the beginning of the study to 92% at the end. Density during this period doubled due to the partitioning of larger colonies into more, smaller colonies. Models suggest that maintenance of conditions present at the end of the study could allow *O. annularis* to maintain about 9% cover over 100 years, but with the return to conditions present from 1993-1998, *O. annularis* could return to coverage similar to that of 1988 (33% cover) in about 15 years (Edmunds 2015).

A demographics study centered around the effects of two major hurricanes that affected the US Virgin Islands in 2017 found that the storms decreased *O. annularis* cover by 1-4% at the two study sites and resulted in the transition of colonies to smaller size classes (Edmunds 2019). In addition, the storms killed 27% of colonies in the smallest size class at one site and 5% at the other. The study concluded that with the low cover of *O. annularis* distributed among many small colonies, future disturbances may play a more important role in loss of the few remaining genotypes rather than further depressing coral cover (Edmunds 2019).

A demographic study of *O. annularis* was undertaken at two sites in Puerto Rico. From 2012 to 2014, 100 colonies were followed for growth, survival, and recruitment and used to estimate population growth rates (Soto-Santiago et al. 2017). Survival overall was 70%, and no recruits were found during the study period. Population growth rates were below equilibrium in both years (range 0.67 to 0.82) and declined between the first and second years of the study. The most frequent condition was to remain in the smallest size class ($\leq$ 50 cm^2), and growth was mainly from small to medium (51-150 cm^2) colonies. More colonies shrank than grew to larger size classes. The study suggests that even in the absence of major disturbance, the vital rates (growth survival, and recruitment rates) of *O. annularis* can be susceptible to local variations in environmental parameters (Soto-Santiago et al. 2017).

Recruitment of *O. annularis* is still extremely low. In a survey of juvenile corals at Mona Island, Puerto Rico in 2012, only 7 juvenile *O. annularis* colonies were observed out of the 347 corals found across 465 surveyed quadrats (Hernández-Delgado et al. 2014). None of the demographic studies cited above indicated observing *O. annularis* recruits during their study period.

2.3.3.1.3 Genetics, genetic variation, or trends in genetic variation (e.g., loss of genetic variation, genetic drift, inbreeding, etc.):

There was one new publication examining genetic variation within colonies of *O. annularis*. Ramets of fragmented *O. annularis* and intact *O. franksi* colonies were sampled along a transect at a site in Panama and analyzed using microsatellites (Olsen et al. 2019). Colonies of different sizes and different depth distributions were targeted. Samples containing genetic deviations were found in 13 of the 29 corals tested (45%). Two of these corals may have experienced chimerism where two distinct genotypes fused. Deviations in the other 11 corals were due to somatic mutations, and the prevalence of mutations was associated positively with colony size and negatively with coral depth. The authors believe this trend is a result of the greater number of somatic DNA duplication events experienced by larger corals and to abiotic factors correlated with depth, such as temperature, which may influence mutation rates (Olsen et al. 2019).

2.3.3.1.4 Spatial distribution, trends in spatial distribution (e.g. increasingly fragmented, increased numbers of corridors, etc.), or historic range (e.g. corrections to the historical range, change in distribution of the species' within its historic range, etc.):

In Cuba, surveys were conducted between 2010 and 2016 at 37 sites (9-15 m depth) interspersed among the seven coral reef systems (González-Díaz et al. 2018). *Orbicella* spp. were uncommon to rare, suggesting substantial losses prior to these surveys. However, *Orbicella* spp. were moderately common at Península Ancón and Jardines de la Reina (González-Díaz et al. 2018).

Unpublished NCRMP monitoring data show that percentage of sites where *O. annularis* was present between 2014 and 2019 was variable but ranged between about 15% and 30% in Puerto Rico and the Virgin Islands (Appendix 2, Figure 68). Between 2014 and 2019, *O. annularis* was present at about 10% to 30% of sites in the Florida Keys, at <5% of sites in southeast Florida, and at <10% of sites in the Dry Tortugas. (Appendix 2, Figure 68).

2.3.3.1.5 Habitat or ecosystem conditions (e.g., amount, distribution, and suitability of the habitat or ecosystem):

One study examined the effects of filamentous turf algae on *O. annularis* reproduction. In an experiment that tested short term (2.5 months) and long term (7-10 months) removal of filamentous turf algae from *O. annularis* colonies, mature gametes were larger in size and present in a higher percentage (almost twice as many) in the filamentous algal removal treatments. This shows the negative effects of filamentous turf algae on reproduction of a species that already exhibits almost non-existent sexual recruitment (Cetz-Navarro et al. 2015).

Two studies examined the effects of coastal development in the US Virgin Islands on *O. annularis*. Coral reef condition on the south shore of St. Thomas was assessed at various distances from Charlotte Amalie, the most densely populated city on the island, and compared to an integrated stressor index incorporating landscape development intensity, sedimentation threat, and water quality impairment (Oliver et al. 2018). Density of *O. annularis* was negatively correlated with the stressor index indicating the sensitivity of this species to coastal development and associated water quality degradation. A different study in St. Thomas examined tissue lesion regeneration rates of *O. annularis* along an environmental gradient with varying distances from developed areas, which were hypothesized to have poorer water quality conditions (Sabine et al. 2015). Water flow and turbidity were found to have the greatest influence on recovery rates; the site with the highest turbidity and least water flow had recovery rates three times slower than the least impacted site with low turbidity, high flow, and low levels of anthropogenic disturbance.

2.3.3.2 Five-Factor Analysis (threats, conservation measures, and regulatory mechanisms)

2.3.3.2.1 Present or threatened destruction, modification or curtailment of its habitat or range:

Loss of recruitment habitat continues to be a threat to Caribbean corals, including *O. annularis*. The presence of algae can inhibit settlement of coral larvae, and in many locations in the Caribbean, there has been a shift from coral dominated to algal dominated reefs partially attributed to the loss of herbivores, including the Caribbean-wide die-off of the long spined sea urchin *D. antillarum* and the trophic effects of over-fishing. There is no new information about the magnitude of this threat to *O. annularis*.

2.3.3.2.2 Overutilization for commercial, recreational, scientific, or educational purposes:

Although *O. annularis* is susceptible to collection and trade, it is a low threat that did not contribute to its status. No new information indicates a change in the magnitude of this threat.

2.3.3.2.3 Disease or predation:

Disease

There have been new studies examining the transmission of white plague disease in O. *annularis*. One laboratory study found that white plague disease was transmissible both through water transport and through predation by the corallivorous snail *C. abbreviata*, and not through contact with macroalgae; transport by water resulted in more frequent and faster transmission as well as higher rates of tissue loss (Clemens and Brandt 2015). A second study examined the rates of transmission of white plague disease from *O. franksi* to *O. annularis* and found that 83% of *O. annularis* colonies were infected within six days (Williams et al. 2020b). Additionally, *O. annularis* was more susceptible and infected faster than two other non-ESA listed coral species tested. These studies support the characterization of *O. annularis* as highly susceptible to disease.

Since the listing, a new disease has emerged that impacts at least 24 Caribbean coral species, including five of the seven ESA-listed species (does not affect *A. cervicornis* or *A. palmata*) (Florida Coral Disease Response Research & Epidemiology Team 2018). This disease, called stony coral tissue loss disease (SCTLD), was first observed in Miami, Florida in 2014 and then spread throughout the Florida reef tract over the next several years (Neely 2018; Precht et al. 2016). It has continued to spread throughout much of the Caribbean and has been observed along the Mesoamerican Reef, Bahamas, Greater Antilles, and as far south as St. Lucia in the Lesser Antilles (see https://www.agrra.org/coral-disease-outbreak/ for a map of confirmed sightings of SCTLD in the greater Caribbean). The disease is unprecedented in the temporal and geographic scope as well as the number of susceptible species, prevalence, and rates of mortality (Neely 2018; Precht et al. 2016). In almost all affected species, tissue loss occurs rapidly and leads to full colony mortality. The disease appears to be both water-born and transmissible through direct contact (Neely 2018). Unlike other coral diseases, it does not appear to be seasonal or subside with cooling water temperature.

Orbicella annularis has been described as intermediately susceptible to SCTLD based on the observation that it is not one of the first species to exhibit disease once a site becomes infected (Florida Coral Disease Response Research & Epidemiology Team 2018). However, prevalence can be high in some locations and may increase over time. Because almost all colonies succumb completely to SCTLD, prevalence is a good indicator of mortality rate (Precht et al. 2016). In surveys of 14 sites off southeast Florida between 2013 and 2015, the prevalence of SCTLD was 77% of *O. annularis* colonies surveyed (Precht et al. 2016). In surveys in southeast Florida after Hurricane Irma in 2017, disease was observed affecting 67% of *O. annularis* colonies and impacted 11% of sites surveyed (243 out of 2,130 (Walker 2018). In surveys along 82 sites in Mexico, prevalence of SCTLD was about 10% for *O.*

annularis (Alvarez-Filip et al. 2019), and in the Bahamas, prevalence was 8% at Grand Bahama and 4% at New Providence (Dahlgren et al. 2021). In the US Virgin Islands long-term monitoring transects, overall initial prevalence of SCTLD in *O. annularis* was about 8% when disease was first reported at a site (Brandt et al. 2021). However, over time, prevalence increased to 100%, reducing the number of colonies in the transects from 81 colonies present between 2005 and 2018 before SCTLD arrived to only 3 by the end of the study (Brandt et al. 2021).

Predation

Orbicella annularis has low susceptibility to predation, and there is no new information related to this threat.

2.3.3.2.4 Inadequacy of existing regulatory mechanisms:

The threats related to global climate change, including bleaching from ocean warming, ocean acidification, and increased disease (Maynard et al. 2015), pose the greatest potential extinction risk to corals and in the last review were evaluated with sufficient certainty out to the year 2100. We relied on information in the Intergovernmental Panel on Climate Change (IPCC) Fifth Assessment Report (AR5), Climate Change 2013: The Physical Science Basis (IPCC 2013), commonly referred to as the Working Group I Report (WGI). This report presented four Representative Concentration Pathways (RCPs) to simulate future climate change, and we evaluated extinction risk using RCP8.5 which represented the high emissions pathway we were currently on.

The IPCC is now in its sixth assessment cycle (AR6) and has released the WGI report Climate Change 2021: The Physical Science Basis (IPCC 2021) that addresses the most updated physical understanding of the climate system and climate change. The latest report indicates that greenhouse gases have continued to increase in the atmosphere since the 2011 measurements reported in AR5. Strong warming has been observed since 2012, and 2016–2020 was the hottest five-year period recorded since at least 1850. Global surface temperature was 1.09°C higher in 2011–2020 than in 1850–1900. On the current emissions trajectory (RCP8.5), the onset of annual severe coral bleaching in the Caribbean is predicted to occur in 2040-2043 with some regional variation (van Hooidonk et al. 2015); under RCP4.5, which represents lower emissions mid-century than will occur if pledges made following the 2015 Paris Climate Change Conference (COP21) become reality, annual coral bleaching is predicted to occur 11 years later, thus doing little to give corals more time to adapt and acclimate (van Hooidonk et al. 2016). Therefore, existing regulatory mechanisms have continued to be inadequate to protect against climate change and the threat it poses to corals due to ocean warming, ocean acidification, and related increases in disease.

AR6 considers 5 greenhouse gas scenarios: very low (SSP1-1.9), low (SSP1-2.6), intermediate (SSP2-4.5), high (SSP3-7.0), and very high (SSP5-8.5). The report indicates that global surface temperature will continue to increase until at least 2050 under all five emission scenarios considered in the report. Crossing the 2°C global warming level in the period 2041–2060 is "very likely" to occur under the very high emissions scenario (SSP5-8.5), "likely" to occur under the high emissions scenario (SSP3-7.0), and "more likely than not" to occur in the intermediate emissions scenario (SSP2-4.5). In the nearer term (2021-2040), the 1.5°C global warming level is "very likely" to be exceeded under the very high GHG emissions scenario (SSP5-8.5), "likely" to be exceeded under the intermediate and high emissions scenarios (SSP2-4.5 and SSP3-7.0), "more likely than not" to be exceeded under the low emissions scenario (SSP1-2.6) and "more likely than not" to be reached under the very low emissions scenario (SSP1-1.9). With additional global warming, there is high confidence that the frequency of marine heatwaves will continue to increase, particularly in the tropical ocean. There is "likely" to be a global increase in marine heatwaves of 2–9 times in 2081–2100 compared to 1995–2014 under the low emissions scenario (SP1-2.6) and 3–15 times under the very high emissions scenario (SSP5-8.5). Thus, projected warming is expected to increase in the future.

2.3.3.2.5 Other natural or manmade factors affecting its continued existence:

Ocean Warming

There have been recent studies examining the effects of bleaching on the species and species complex (*O. annularis*, *O. faveolata*, and *O. franksi*). Long-term monitoring of 16 permanent monitoring sites in Puerto Rico showed the 2005 bleaching event resulted in extreme reductions in coral cover of the species complex; *Orbicella* spp. ranged from approximately 9% to 25% cover before the bleaching event to approximately <2% to 7% up to 10 years after the event (Garcia-Sais et al. 2017). At some sites, partial recovery of coral cover was observed by 2015 but not to the levels observed prior to bleaching. Some sites even experienced a loss in dominance of the species complex (Garcia-Sais et al. 2017).

Another study looked at the long-term effects of bleaching on *O. annularis*, *O. faveolata*, and *O. franksi* reproduction. After bleaching events that occurred in Panama in 2005 and 2010, reduced spawning was observed in all species and persisted for several years (Levitan et al. 2014). Both bleached and unbleached colonies had reduced probability of spawning for several years following the 2010 bleaching event even though bleaching did not alter coral survival or tissue loss. However, bleached colonies were less likely to spawn than those that did not visibly bleach. *Orbicella annularis* was most affected by bleaching but recovered the ability to spawn sooner than *O. franksi,* which was least affected by the bleaching event. The authors concluded that corals that recover from bleaching events can experience long-term reduction in reproductive output over time scales that can bridge the interval between subsequent bleaching events (Levitan et al. 2014).

Acidification

Orbicella annularis is susceptible to ocean acidification resulting from climate change. However, there is no new species-specific information related to this threat.

Sedimentation

Orbicella annularis is susceptible to sedimentation and turbidity. However, there is no new species-specific information related to this threat.

Nutrients

Orbicella annularis is susceptible to nutrients. However, there is no new species-specific information related to this threat.

2.3.3.3 Synthesis

At the time of listing as threatened, *O. annularis*' common occurrence, distribution, and life history strategy, in which large, long-lived colonies were able to buffer losses and allow the species to persist despite slow growth and extremely low recruitment, were determined to moderate the species' vulnerability to extinction. It was expected that this buffering capacity would decrease with declining populations as threats were predicted to increase into the future. It was not considered as endangered at the time of listing because its population was not so low or fragmented to indicate depensatory processes were in effect, because exposure to threats was moderated by its inhabitation of multiple habitats across a moderate depth range that would experience highly variable thermal regimes at local and regional scales, and because there was some evidence that symbiont shuffling could occur and provide some bleaching resistance.

Since the listing, *O. annularis* populations have continued to decline in abundance, dominance, and cover in some locations, such as Cuba, the Florida Keys, and the US Virgin Islands, while others like the Dry Tortugas and deeper areas of the US Virgin Islands appear to be more stable. No trend information was found for areas outside the US Caribbean and Cuba. Partial mortality of larger colonies has continued to result in a shift to smaller size classes. Periods of growth may occur between disturbance events, but the frequency of events prevents recovery to larger size classes. Although considered common at the time of listing, the presence of *O. annularis* colonies is becoming less common in some locations. The percentage of sites where *O. annularis* is present ranges from about 5% to 30% in locations for which data are available with no overall obvious decreasing trends.

Orbicella annularis was categorized as highly susceptible to coral disease at the time of listing, and the arrival of SCTLD has had additional detrimental impacts on *O. annularis*. Though the species is considered intermediately susceptible to SCTLD because it is not one of the first species to show signs of the disease when a site first becomes affected, prevalence and resulting mortality can be very high, as demonstrated in southeast Florida and the US Virgin Islands, once the disease becomes established. Whole colony mortality is common with SCTLD, and the disease appears to be moving across the Caribbean, affecting more and more locations, with no signs of seasonality or abatement. Thus, both the scope and severity of disease have increased in relation to the threat they pose to *O. annularis* since the time of listing.

At the time of listing, *O. annularis* was described as highly susceptible to bleaching. Additional studies since that time have supported the observation of high mortality of the species after bleaching events and reduced reproduction several years after anomalously high water temperatures and bleaching. Thus, ocean warming is still a high importance threat to *O. annularis*.

In the listing determination, *O. annularis* was described as likely highly susceptible to acidification, and there has been no new species-specific information related to this threat.

At the time of listing, *O. annularis* was considered to have some susceptibility to the trophic effects of fishing that can result in the proliferation of algae that can compete for space on the reef and hinder coral settlement. Competition from algae was shown to have effects on *O. annularis* ranging from changes in the microbiome to reduction in fecundity. Since the listing, a new study has shown reduced fecundity of *O. annularis* and smaller gamete sizes in the presence of filamentous turf algae, supporting the earlier findings of some susceptibility of *O. annularis* to the trophic effects of fishing.

In the listing determination, *O. annularis* was considered highly susceptible to sedimentation and nutrients. New studies in the US Virgin Islands have found that *O. annularis* is negatively affected by coastal development and associated decreased water quality. Density of *O. annularis* was negatively correlated with a stressor index indicating the species' sensitivity to sedimentation and water quality. Additionally, tissue regeneration rates were lower under conditions of higher turbidity and lower water flow. These findings support the conclusion that *O. annularis* is highly sensitive to sedimentation and nutrients.

Other threats to *O. annularis* in the listing determination include low susceptibility to predation and collection and trade and some susceptibility to sea level rise. There is no new species-specific information related to these threats.

In summary, populations of *O. annularis* and the buffering capacity of its life history strategy continue to decrease, and available information indicates it is becoming less common in some locations. Despite these declines, there is no indication that *O. annularis* populations are so low or fragmented that depensatory processes are affecting the species, and the species still inhabits its historical range and maintains its historical distribution, modulating its vulnerability to extinction. The susceptibility of *O. annularis* to threats identified at the time of listing has not changed, though the emergence of SCTLD has substantially raised the vulnerability of *O. annularis* to disease. Based on all these factors, *O. annularis* continues to be at risk of becoming an endangered species in the foreseeable future but does not appear to be currently at risk of extinction. Thus, no change in status is recommended at this time.

2.3.4 ORBICELLA FRANKSI

2.3.4.1 Biology and Habitat

2.3.4.1.1 New information on the species' biology and life history:

New studies provide updated information on the larval competency period and growth rates of *O. franksi*. In a laboratory study, *O. franksi* larvae were not competent to settle until >20 days post fertilization and remained competent up to 120 days post fertilization (Davies et al. 2017). In a study of growth rates on reefs in the US Virgin Islands, *O. franksi* was observed to have slower skeletal growth rates (~0.2 cm yr^{-1}) below 30 m compared to ~1 cm yr^{-1} in shallower habitats (Groves et al. 2018). Slower growth rates in mesophotic reefs suggest that recovery from disturbances will be slow and affect the buffering capacity and ability to serve as refugia for highly stressed shallow water habitats (Groves et al. 2018).

2.3.4.1.2 Abundance, population trends (e.g. increasing, decreasing, stable), demographic features (e.g., age structure, sex ratio, family size, birth rate, age at mortality, mortality rate, etc.), or demographic trends:

Unpublished monitoring data from long-term benthic monitoring programs show that between 2014 and 2019, live tissue area of *O. franksi* was relatively stable in Florida, though regional trends indicated an overall decline in the Florida Keys and an increase in the Dry Tortugas (southeast Florida close to 0) (Appendix 2, Figure 97). Average density in Florida was also relatively stable when averaged across all transects, ranging from a low of 0.04 colonies m^{-2} in 2015 to a high of 0.07 colonies m^{-2} in 2018 (Appendix 2, Figure 99). Density in the Dry Tortugas was higher than in the Florida Keys and southeast Florida and increased between 2014 and 2019 (Appendix 2, Figure 99).

Unpublished data from the US Virgin Islands long-term monitoring program show cover of *O. franksi* was relatively stable between 2014 and 2020, hovering around 4.5% to 5.5% (Appendix 2, Figure 110). If these sites are evaluated by depth classes, most depths show stable or increasing cover of *O. franksi* between 2014 and 2017 and then a decrease in 2018 that either stabilized or continued to decline (Appendix 2, Figure 110). The exception was sites 21-30 m in depth that showed a decline in 2019 but then an increase in 2020 (though note that not all sites were surveyed in 2020).

Unpublished monitoring data from randomly surveyed sites (different sites surveyed each year) include colony size and partial mortality. Mean colony diameter appeared relatively stable at about 30 cm in Puerto Rico and the US Virgin Islands in 2014-2020 while the Dry Tortugas had stable mean colony diameter slightly higher at approximately 40 cm (Appendix 2, Figure 105). Southeast Florida and the Florida Keys exhibited more variability in mean colony diameter among survey years, but in the most recent survey in 2018, mean colony diameter was slightly less than 40 cm in the Florida Keys and slightly over 60 cm in southeast Florida (Appendix 2, Figure 105). Mean partial mortality of *O. franksi* colonies was about 15-30% in the Dry Tortugas, US Virgin Islands, and Puerto Rico (Appendix 2, Figure 105). In the Florida Keys and southeast Florida, partial colony mortality was more variable with the average ranging from about 15-50% in the Florida Keys and from about 20-40% in southeast Florida (Appendix 2, Figure 105).

2.3.4.1.3 Genetics, genetic variation, or trends in genetic variation (e.g., loss of genetic variation, genetic drift, inbreeding, etc.):

One new publication examined genetic variation within colonies of *O. franksi*. Ramets of fragmented *O. annularis* and intact *O. franksi* colonies were sampled along a transect at a site in Panama and analyzed using microsatellites (Olsen et al. 2019). Colonies of different sizes and different depth distributions were targeted. Samples containing genetic deviations were found in 13 of the 29 corals tested (45%). Two of these corals may have experienced chimerism where two distinct genotypes fused. Deviations in the other 11 corals were due to somatic mutations, and the prevalence of mutations was associated positively with colony size and negatively with coral depth. The authors believe this trend is a result of the greater number of somatic DNA duplication events experienced by larger corals and to abiotic factors correlated with depth, such as temperature, which may influence mutation rates (Olsen et al. 2019).

2.3.4.1.4 Spatial distribution, trends in spatial distribution (e.g. increasingly fragmented, increased numbers of corridors, etc.), or historic range (e.g. corrections to the historical range, change in distribution of the species' within its historic range, etc.):

NOAA Fisheries received some new information about the distribution of *Orbicella* spp. in Florida and near the Flower Garden Banks National Marine Sanctuary (Gulf of Mexico off the Texas coast) through the critical habitat designation process. Although *O. franksi* can occur in depths up to 90 m, the species has not been observed at mesophotic depths (>40 m) in surveys conducted in the Florida Keys, Dry Tortugas, or Pulley Ridge in the Gulf of Mexico (pers. comm, John Reed (Florida Atlantic University) to Jennifer

Moore, email dated 06/09/16; Reed and Farrington 2021a). In addition to presence in East and West Flower Garden Banks, *Orbicella* spp. have been observed at Bright, McGrail, and Geyer Banks in the Gulf of Mexico off the coast of Texas; the depth distribution around the Flower Garden Banks National Marine Sanctuary is 16-90 m (pers. comm. Flower Garden Banks National Marine Sanctuary public comments to Jennifer Moore, email dated 02/02/21).

There were new studies on the distribution of *O. franksi* or the *Orbicella* species complex in the Greater Antilles. In a survey of 52 stations in St. Croix in 2007 and 52 stations in St. Thomas and St. John in 2009, *O. franksi* was observed in 12% of stations in St. Croix and 50% in St. Thomas and St. John (Fisher et al. 2014). This species was present in a lower proportion of stations than either *O. annularis* (31-65% of stations) or *O. faveolata* (60-73% of stations). In Cuba, surveys were conducted in 37 sites (9-15 m depth) interspersed among the seven coral reef systems between 2010 and 2016 (González-Díaz et al. 2018). *Orbicella* spp. were uncommon to rare, suggesting substantial losses prior to these surveys. However, *Orbicella* spp. were moderately common at Península Ancón and Jardines de la Reina (González-Díaz et al. 2018).

There is also some unpublished information from benthic monitoring programs in the US. In randomly sampled sites (different sites surveyed each year), the presence of *O. franksi* was variable from year to year in Florida, the US Virgin Islands, and Puerto Rico, but no regions showed any overall patterns of decreased presence between 2014 and 2019 (Appendix 2, Figures 103 and 104). *Orbicella franksi* was present at approximately 30-50% of sites in the Dry Tortugas and US Virgin Islands, 5-30% of sites in the Florida Keys, 15-20% in Puerto Rico, and 0-5% in southeast Florida (Appendix 2, Figure 104). In a separate survey conducted in Puerto Rico in 2018 after the 2017 hurricanes, *O. franksi* was present in about half of the sites visited (Appendix 2, Figure 108).

2.3.4.1.5 Habitat or ecosystem conditions (e.g., amount, distribution, and suitability of the habitat or ecosystem):

There was a study examining the effects of coastal development in the US Virgin Islands on *O. franksi*. Coral reef condition on the south shore of St. Thomas was assessed at various distances from Charlotte Amalie, the most densely populated city on the island, and compared to an integrated stressor index incorporating landscape development intensity, sedimentation threat, and water quality impairment (Oliver et al. 2018). Density of *O. franksi* was negatively correlated with the stressor index, indicating the sensitivity of this species to coastal development and associated water quality degradation.

2.3.4.2 Five-Factor Analysis (threats, conservation measures, and regulatory mechanisms)

2.3.4.2.1 Present or threatened destruction, modification or curtailment of its habitat or range:

Loss of recruitment habitat continues to be a threat to Caribbean corals, including *O. franksi*. The presence of algae can inhibit settlement of coral larvae, and in many locations in the Caribbean, there has been a shift from coral dominated to algal dominated reefs partially attributed to the loss of herbivores, including the Caribbean-wide die-off of the long spined sea urchin *D. antillarum* and the trophic effects of over-fishing. There is no new information about the magnitude of this threat to *O. franksi*.

2.3.4.2.2 Overutilization for commercial, recreational, scientific, or educational purposes:

Although *O. franksi* is susceptible to collection and trade, it is a low threat that did not contribute to its status. No new information indicates a change in the magnitude of this threat.

2.3.4.2.3 Disease or predation:

Disease

Since the listing, the new SCTLD has emerged impacting at least 24 Caribbean coral species, including five of the seven ESA-listed species (Florida Coral Disease Response Research & Epidemiology Team 2018). SCTLD was first observed in Miami, Florida in 2014 and then spread throughout the Florida reef tract over the next several years (Neely 2018; Precht et al. 2016). It has continued to spread throughout much of the Caribbean and has been observed along the Mesoamerican Reef, Bahamas, Greater Antilles, and as far south as St. Lucia in the Lesser Antilles (see https://www.agrra.org/coral-disease-outbreak/ for a map of confirmed sightings of SCTLD in the greater Caribbean). The disease is unprecedented in the temporal and geographic scope as well as the number of susceptible species, prevalence, and rates of mortality (Neely 2018; Precht et al. 2016). In almost all affected species, tissue loss occurs rapidly and leads to full colony mortality. Because almost all colonies succumb completely to SCTLD, prevalence is a good indicator of mortality rate (Precht et al. 2016). The disease appears to be both water-born and transmissible through direct contact (Neely 2018).

Orbicella franksi is considered intermediately susceptible to SCTLD because it is not one of the first species to contract the disease once a site is infected (Florida Coral Disease Response Research & Epidemiology Team 2018). In surveys in southeast Florida after Hurricane Irma in 2017, prevalence of disease was 14% of *O. franksi* colonies, and SCTLD was present at 11% (243 out of 2,130) of sites surveyed (Walker 2018). At two sites in the Bahamas, prevalence of SCTLD in *O. franksi* was 13% at Grand Bahama and 2% at

New Providence (Dahlgren et al. 2021). In the USVI long-term monitoring transects, overall initial prevalence of SCTLD in *O. faveolata*/*O. franksi* was about 12% when disease was first reported at a site (Brandt et al. 2021). However, over subsequent surveys, prevalence rose as high as about 45%, reducing the abundance of *O. faveolata*/*O. franksi* colonies from 684 colonies in the transects between 2005 and 2018 before SCTLD arrived to just 12 colonies by the end of the study (Brandt et al. 2021).

Predation

Orbicella franksi has low susceptibility to predation, and there is no new information related to this threat.

2.3.4.2.4 Inadequacy of existing regulatory mechanisms:

The threats related to global climate change, including bleaching from ocean warming, ocean acidification, and increased disease (Maynard et al. 2015), pose the greatest potential extinction risk to corals and in the last review were evaluated with sufficient certainty out to the year 2100. We relied on information in the Intergovernmental Panel on Climate Change (IPCC) Fifth Assessment Report (AR5), Climate Change 2013: The Physical Science Basis (IPCC 2013), commonly referred to as the Working Group I Report (WGI). This report presented four Representative Concentration Pathways (RCPs) to simulate future climate change, and we evaluated extinction risk using RCP8.5 which represented the high emissions pathway we were currently on.

The IPCC is now in its sixth assessment cycle (AR6) and has released the WGI report Climate Change 2021: The Physical Science Basis (IPCC 2021) that addresses the most updated physical understanding of the climate system and climate change. The latest report indicates that greenhouse gases have continued to increase in the atmosphere since the 2011 measurements reported in AR5. Strong warming has been observed since 2012, and 2016–2020 was the hottest five-year period recorded since at least 1850. Global surface temperature was 1.09°C higher in 2011–2020 than in 1850–1900. On the current emissions trajectory (RCP8.5), the onset of annual severe coral bleaching in the Caribbean is predicted to occur in 2040-2043 with some regional variation (van Hooidonk et al. 2015); under RCP4.5, which represents lower emissions mid-century than will occur if pledges made following the 2015 Paris Climate Change Conference (COP21) become reality, annual coral bleaching is predicted to occur 11 years later, thus doing little to give corals more time to adapt and acclimate (van Hooidonk et al. 2016). Therefore, existing regulatory mechanisms have continued to be inadequate to protect against climate change and the threat it poses to corals due to ocean warming, ocean acidification, and related increases in disease.

AR6 considers 5 greenhouse gas scenarios: very low (SSP1-1.9), low (SSP1-2.6), intermediate (SSP2-4.5), high (SSP3-7.0), and very high (SSP5-8.5). The report indicates that global surface temperature will continue to increase until at least 2050 under all five emission scenarios considered in the report. Crossing the 2°C global warming level in the period 2041–2060 is “very likely” to occur under the very high emissions scenario (SSP5-8.5), “likely” to occur under the high emissions scenario (SSP3-7.0), and “more likely than not” to occur in the intermediate emissions scenario (SSP2-4.5). In the nearer term (2021-2040), the 1.5°C global warming level is “very likely” to be exceeded under the very high GHG emissions scenario (SSP5-8.5), “likely” to be exceeded under the intermediate and high emissions scenarios (SSP2-4.5 and SSP3-7.0), “more likely than not” to be exceeded under the low emissions scenario (SSP1-2.6) and “more likely than not” to be reached under the very low emissions scenario (SSP1-1.9). With additional global warming, there is high confidence that the frequency of marine heatwaves will continue to increase, particularly in the tropical ocean. There is “likely” to be a global increase in marine heatwaves of 2–9 times in 2081–2100 compared to 1995–2014 under the low emissions scenario (SP1-2.6) and 3–15 times under the very high emissions scenario (SSP5-8.5). Thus, projected warming is expected to increase in the future.

2.3.4.2.5 Other natural or manmade factors affecting its continued existence:

Ocean Warming

There have been several recent studies examining the effects of bleaching on the species and species complex (*O. annularis*, *O. faveolata*, and *O. franksi*). Long-term monitoring of 16 permanent monitoring sites in Puerto Rico showed that the 2005 bleaching event resulted in extreme reductions in coral cover of the species complex; *Orbicella* spp. ranged from approximately 9% to 25% cover before the bleaching event to approximately <2% to 7% up to 10 years after the event (Garcia-Sais et al. 2017). At some sites, partial recovery of coral cover was observed by 2015 but not to the levels observed prior to bleaching. Some sites even experienced a loss in dominance of the species complex (Garcia-Sais et al. 2017).

A study in Panama followed colonies of *O. franksi* (n=52) during the 2005 bleaching event and for 8 years after (2005-2013). Bleached colonies suffered a mean tissue loss of 26% per colony 9 months post bleaching (Neal et al. 2017). They later recovered to net positive annual growth (mean 2% annual growth) until the next bleaching event in 2010. Colonies that previously did not bleach in 2005 suffered higher tissue loss than those that previously bleached, indicating a potential acclimation response. However, there was substantial net tissue loss of all bleached colonies over the course of the study, indicating this species may not be able to recover from losses due to increased frequency expected for bleaching events (Neal et al. 2017).

Another study looked at the long-term effects of bleaching on *O. annularis*, *O. faveolata*, and *O. franksi* reproduction. After bleaching events in Panama in 2005 and 2010, reduced spawning was observed in all species and persisted for several years (Levitan et al. 2014). Both bleached and unbleached colonies had reduced probability of spawning for several years following the 2010 bleaching event even though bleaching did not alter coral survival or tissue loss, though bleached colonies were less likely to spawn than those that did not visibly bleach. Although *O. franksi* was least affected by bleaching, it took longer to recover the ability to spawn than *O. annularis* which was most affected by bleaching. The authors concluded that corals that recover from bleaching events can experience long-term reduction in reproduction, over time scales that can bridge the interval between subsequent bleaching events (Levitan et al. 2014).

In a study of hydrogen peroxide effects on recruitment of *O. franksi*, hydrogen peroxide concentrations of 100 µm l^{-1} or greater caused a significant reduction in fertilization of gametes, metamorphosis, and larval settlement (Ross et al. 2017). Heat stress influences internal production of hydrogen peroxide, which impacts coral settlement and has the capacity to affect coral recruitment under a changing climate (Ross et al. 2017).

Colonies of *O. franksi* from Panama and Bermuda were studied to quantify the thermal sensitivity of important physiological functions in locations close to the northern and southern extent of the species' range (Silbiger et al. 2019). The populations with different thermal histories responded differently to acute warming. The population in warmer Panama was more thermally tolerant, exhibiting a higher thermal optimum and critical maximum, than the cooler Bermuda population, which could be a result of thermal adaptation or acclimation. The Panama population exhibited higher gross photosynthesis rates overall. Within the populations, calcification was more sensitive to temperature, followed by photosynthesis, and then respiration. Results indicate that the species may be able to survive slight increases in temperature (e.g. ~1-2°C) but they would still experience declines and possibly loss of ecological functions related to fitness (Silbiger et al. 2019).

Acidification

Oribicella franksi is susceptible to ocean acidification as a result of climate change. However, there is no new species-specific information related to this threat.

Sedimentation

Oribicella franksi is susceptible to sedimentation and turbidity. However, there is no new species-specific information related to this threat.

Nutrients

Oribicella franksi is susceptible to nutrients. However, there is no new species-specific information related to this threat.

2.3.4.3 Synthesis

At the time of listing as threatened, *O. franksi*'s common occurrence, distribution, and life history strategy, in which large, long-lived colonies were able to buffer losses and allow the species to persist despite slow growth and extremely low recruitment, were determined to moderate the species' vulnerability to extinction. It was expected that this buffering capacity would decrease with declining populations as threats were predicted to increase into the future. It was not considered as endangered at the time of listing because its population was not so low or fragmented to indicate depensatory processes were in effect, because exposure to threats was moderated by its inhabitation of multiple habitats across a wide depth range, including both shallow and mesophotic depths, that would experience highly variable thermal regimes at local and regional scales, and because some populations were experiencing stability over decadal time scales.

New information since the time of listing suggests that *O. franksi* is still relatively common though may have become less common in certain locations such as those around Cuba. Although it can occur at deeper depths, *O. franksi* has not been observed in mesophotic areas of the Florida Keys, Dry Tortugas, or Pulley Ridge in the Gulf of Mexico. However, it has been observed on additional banks near the Flower Gardens in the Gulf of Mexico. Since the listing, live cover of *O. franksi* has decreased in some locations such as the Florida Keys but has remained stable in others such as the Dry Tortugas and US Virgin Islands. Monitoring data show that average colony size and density vary by location but seem to be relatively stable with partial mortality ranging from about 15-50%. The new information suggests that *O. franksi* continues to have mixed population trends with some decline and some stability.

At the time of listing, *O. franksi* was considered highly susceptible to ocean warming. New information since the listing confirms that ocean warming and subsequent bleaching can cause high tissue loss of *O. franksi*. In addition, new information shows that anomalously high water temperatures and bleaching can affect *O. franksi* reproduction through reductions in spawning that can last for several years. Additonal information indicates *O. franksi* may be capable of acclimation or an adaptative response to warmer water temperatures. Colonies living in different thermal regimes showed different responses to warming temperatures with colonies from warmer locations displaying a higher thermal tolerance than those living in cooler locations. In another study, colonies that bleached in a prior bleaching event suffered lower tissue loss in a subsequent bleaching event 5 years later than those that did not bleach in the first event, though net tissue loss for all bleached colonies was high. Despite the potential for acclimation or adaptation, recovery rates indicate that this species will likely not be able to recover from losses due to increased frequency expected for bleaching events. Thus, new information confirms that *O. franksi* is highly susceptible to ocean warming.

In the listing determination, *O. franksi* was considered to be highly susceptible to disease. Since the listing, SCTLD has emerged as a new disease to which *O. franksi* has been described as intermediately susceptible since it is not one of the first species to become infected once SCTLD arrives at a site. Prevalence of this disease in *O. franksi* appears to be less than 15% soon after SCTLD arrives at a site but can increase with time as has been observed in the US Virgin Islands. Because total colony mortality often results from SCTLD and because SCTLD has been progressing to new sites around the Caribbean without signs of slowing or any seasonal pattern, both the scope and severity of disease have increased in relation to the threat they pose to *O. franksi* since the time of listing.

The listing determination indicated that *O. franksi* was highly susceptible to sedimentation and nutrients. A new study examining the effects of coastal development found that the abundance of *O. franksi* was negatively correlated to a stressor index, suggesting *O. franksi* is negatively affected by coastal development and the associated reduction in water quality. This study supports the finding that *O. franski* is highly susceptible to sediments and nutrients.

At the time of listing, *O. franksi* was considered likely to be highly susceptible to acidification, likely susceptible to the trophic effects of fishing, have some susceptibility to sea level rise, and have low susceptibility to predation and collection and trade. There has been no new information on the susceptibility of *O. franksi* to any of these threats since the listing.

In summary, although populations of *O. franksi* and the buffering capacity of its life history strategy continue to decrease in some areas, the species has had stable population trends since the listing in other locations. It still inhabits its historical range and maintains its historical distribution. It appears to still be relatively common, and there is no indication that its populations are so low or fragmented that depensatory processes are affecting the species. The susceptibility of *O. franksi* to threats identified at the time of listing has not changed, though the emergence of SCTLD has raised the vulnerability of *O. franski* to disease. Based on all these factors, *O. franksi* continues to be at risk of becoming an endangered species in the foreseeable future but does not appear to be currently at risk of extinction. Thus, no change in status is recommended at this time.

2.3.5 ORBICELLA FAVEOLATA

2.3.5.1 Biology and Habitat

2.3.5.1.1 New information on the species' biology and life history:

There have been new studies on the reproductive biology and early life history of *O. faveolata*. A study of clonality and reproductive compatibility at two sites in the Florida Keys found that one site had higher clonality (10 unique genotypes out of 47 samples) than expected and that the fertilization rate for individual pair-wise crosses was 39% (n=15 crosses), with over half of the individual crosses having fertilization rates of less than 40% (Miller et al. 2018). The authors postulated that both parental incompatibility and low-quality gametes likely contributed to variable fertilization and suggested that the effective population size may be smaller than the total standing population due to clonality and low reproductive compatibility.

In a study of larval competency, the maximum larval longevity (swimming larvae in the absence of settlement cues) of *O. faveolata* was 83 days, with the onset of larval metamorphosis occurring at 4 or 7 days (Miller et al. 2020a). Larval mortality was high up to 4-5 days post spawning and then more stable after that. There was significantly reduced larval survivorship and lower realized settlement under elevated temperatures of 1-1.5°C (Miller et al. 2020a).

In larval settlement experiments in the presence of settlement cues, onset of competency occurred on day 7 post spawning in one study (Alvarado-Chacon et al. 2020) and on days 3-4 in another (Miller et al. 2020a). The latest larval competency was observed at 48 days after spawning (Miller et al. 2020a), and most settlers had acquired zooxanthellae after 37 days (Alvarado-Chacon et al. 2020). Survival after settlement in the lab was 42% after 2 weeks, and no settlers survived after week 3 (Alvarado-Chacon et al. 2020). However, in another study of post-settlement survival, survivorship of *O. faveolata* settled in the lab and placed out on the reef varied from 0-47% over the 6-9 week observation period, but polyps did not bud during this time period (Miller 2014).

A study of symbionts from locations across the greater Caribbean (Florida Keys, Bahamas, Mexico, and Belize) found that *O. faveolata* associated with species of *Symbiodinium* in clades A, B, C, and D (Kemp et al. 2015). There were distinct zonation patterns within colonies. Symbiont distribution was correlated with light availability, cardinal direction, and depth. There were also geographic differences in *Symbiodinium* associations and endemic haplotypes. This ability to host up to four genetically distinct *Symbiodinium* types in predictable patterns has not been reported in any other coral genera. (Kemp et al. 2015).

2.3.5.1.2 Abundance, population trends (e.g. increasing, decreasing, stable), demographic features (e.g., age structure, sex ratio, family size, birth rate, age at mortality, mortality rate, etc.), or demographic trends:

There have been several publications on presence and abundance of *O. faveolata* or the *Orbicella* species complex in the Caribbean from surveys that mostly occurred before 2014 when the species was listed as threatened. In surveys conducted between 2010 and 2016 in the terrace edge habitat (9-15 m), *Orbicella* spp. were uncommon to rare at 37 sites interspersed among the seven coral reef systems in Cuba, suggesting substantial losses prior to the surveys, but *Orbicella* spp. were moderately common at Península Ancón and Jardines de la Reina (González-Díaz et al. 2018). In contrast, *O. faveolata* was among the most dominant species on reefs in the central and southern zones in Mexico in surveys conducted between 1999 and 2000 at 11 sites along 400 km (Rodríguez-Zaragoza and Arias-González 2015). In surveys conducted along Pedro Bank in Jamaica in 2012, coral communities were dominated by small corals, but many sites had high abundances of *O. faveolata* that were generally in good condition (Bruckner et al. 2014). In a survey of 52 stations in St. Croix in 2007 and 52 stations in St. Thomas and St. John in 2009, *O. faveolata* occurred in more than 50% of the stations but had low (<10%) relative abundance, accounting for about 5% of the coral colonies observed (Fisher et al. 2014). *Orbicella faveolata* was observed in 60% of the stations in St. Croix with an average percent live tissue of 52%; *O. faveolata* was present at 73% of stations in St. Thomas and St. John with an average percent live tissue of 66% (Fisher et al. 2014). In a survey of juvenile corals in Mona Island, Puerto Rico in 2012, only 3 juvenile *O. faveolata* colonies were observed out of the 347 juvenile corals found across 465 surveyed quadrats (Hernández-Delgado et al. 2014).

Unpublished monitoring data can provide some more recent insights into *O. faveolata* population trends and abundance since the listing. In permanent monitoring sites in Florida, *O. faveolata* live tissue area decreased between 2014 and 2019 (Appendix 2, Figure 76). Regional trends show more stable live tissue area in the Dry Tortugas and declines in the Florida Keys and southeast Florida (Appendix 2, Figure 76). Overall density of *O. faveolata* in Florida decreased slightly between 2014 and 2019 from about 0.1 colonies m^{-2} to about 0.08 colonies m^{-2} (Appendix 2, Figure 81). Density was highest in the Dry Tortugas but decreased from about 0.3 colonies m^{-2} in 2014 to about 0.2 colonies m^{-2} in 2019 (Appendix 2, Figure 81). In the Florida Keys, density was lower at about 0.1 colonies m^{-2} but was relatively stable between 2014 and 2019 (Appendix 2, Figure 81). Density was lowest in southeast Florida and was typically <0.05 colonies m^{-2} (Appendix 2, Figures 81-82). In monotypic and special habitat sites in Florida, density increased between 2014 and 2019 (Appendix 2, Figure 85).

In stratified random surveys (different sites visited each year), average density of *O. faveolata* was relatively stable at around 0.25 colonies m^{-2} in St. Croix, US Virgin Islands between 2014 and 2019 (Appendix 2, Figure 87), but decreased in St. Thomas/St. John from about 0.2 colonies m^{-2} in 2015 to about 0.1 colonies m^{-2} in 2019 (Appendix 2, Figure 87). In Puerto Rico, average density was more variable and fluctuated between 0.15 and 0.2 colonies m^{-2} between 2015 and 2019 (Appendix 2, Figure 87).

Other data from random surveys include colony size and partial mortality. Average colony size in the US Virgin Islands and Puerto Rico was stable at approximately 30 cm between 2014 and 2019 (Appendix 2, Figure 90). In southeast Florida, average colony size decreased from about 50 to 40 cm between 2014 and 2019 (Appendix 2, Figure 90). The Florida Keys experienced a larger decline from about 70 cm to about 50 cm average colony size between 2014 and 2018, while the Dry Tortugas was more stable over this same time period with an average colony size of about 55 to 60 cm (Appendix 2, Figure 90). Partial colony mortality was generally between 25% and 50% for Florida with increases in southeast Florida and the Dry Tortugas and decreases in the Florida Keys during the 2014 to 2019 time period (Appendix 2, Figure 90). Partial colony mortality in Puerto Rico and the US Virgin Islands was fairly stable at ≤25% between 2014 and 2019 (Appendix 2, Figure 90).

In permanent monitoring stations in the US Virgin Islands, percent cover of *O. faveolata* was relatively stable at about 0.5% between 2015 and 2020 (Appendix 2, Figure 95). Sites deeper than 21 m showed slight declines followed by increases in cover while the shallower sites showed more variable patterns (Appendix 2, Figure 95).

The reproductive performance of *O. faveolata* was investigated in the US Virgin Islands over a depth distribution of 5-40 m to assess the contribution of deeper mesophotic populations to regional larval pools (Holstein et al. 2015). Mesophotic populations produced over an order of magnitude more eggs than nearby shallow populations due to population abundance and polyp fecundity. This finding suggests that mesophotic populations are important as reproductive refugia (Holstein et al. 2015).

2.3.5.1.3 Genetics, genetic variation, or trends in genetic variation (e.g., loss of genetic variation, genetic drift, inbreeding, etc.):

There have been studies examining genetic structure of *O. faveolata* at different spatial scales. In the study conducted across the largest geographic scale, genetic structure of *O. faveolata* was examined across ten sites spanning the wider Caribbean (Rippe et al. 2017). Populations were generally well mixed with notable substructure apparent at local and regional scales. There appears to be an eastern and western *O. faveolata* population with a genetic break at the Mona Passage. However, there was evidence of connectivity between Curaçao and Mexico, suggesting potential dispersal across the southern margin of this genetic break. There was also evidence of a genetic break within the Mesoamerican Barrier Reef that the authors attributed to strong oceanographic patterns that promote larval retention in southern Belize. Florida, the Bahamas, and Mexico had a strong signal of connectivity. Finally, the diverse genetic structure of the Flower Garden Banks suggests this location could be a downstream genetic sink, though low population differentiation between the Flower Garden Banks and the Florida Keys suggests relatively strong connectivity between these two locations (Rippe et al. 2017). The genetic connectivity between the Flower Garden Banks and the Florida Keys provides evidence for the results of a biophysical modeling study that suggests that *O. faveolata* larvae from the Flower Garden Banks could reach the Florida Keys or become entrained in the Gulf of Mexico Loop Current and return to the Flower Garden Banks (Limer et al. 2020).

Orbicella faveolata population structure and genetic diversity were assessed at the regional spatial scale of the Mesoamerican Barrier Reef System and the local scale of Cuba. The study in the Mesoamerican Reef found high genetic diversity and low clonality, as well as low population structure among populations; genotypic diversity was on average 0.98 (Porto-Hannes et al. 2015). A study of population genetics of *O. faveolata* colonies at 5 locations around Cuba showed evidence of differentiation between the northwestern area of Cuba (Colorados Archipelago) and the other reefs (Ulmo-Díaz et al. 2018). Colonies from this northwestern area had the largest number of haplotypes and alleles, suggesting a historically resilient population or gene flow from other areas of the Caribbean (Ulmo-Díaz et al. 2018).

A study was undertaken to examine the frequency of somatic mutations in *O. faveolata*. The study found that somatic mutations can have a frequency up to 50% and generate high intra-colonial genetic diversity (Barfield et al. 2016). However, the somatic mutations are not passed on to gametes (Barfield et al. 2016).

2.3.5.1.4 Spatial distribution, trends in spatial distribution (e.g. increasingly fragmented, increased numbers of corridors, etc.), or historic range (e.g. corrections to the historical range, change in distribution of the species' within its historic range, etc.):

We received some new information about the distribution of *Orbicella* spp. in Florida and near the Flower Garden Banks National Marine Sanctuary (Gulf of Mexico off the Texas coast) through the critical habitat designation process. In surveys focused on mesophotic reef depths (30-100 m) conducted in the Florida Keys, Dry Tortugas, and Pulley Ridge (Gulf of Mexico), the species has only been observed at depths up to 44 m off the northern Florida Keys (pers. comm, John Reed (Florida Atlantic University) to Jennifer Moore, email dated 06/09/16; Reed and Farrington 2021b). In addition to the East and West Flower Garden Banks, *Orbicella* spp. have been observed at Bright, McGrail, and Geyer Banks in the Gulf of Mexico off the coast of Texas; the depth distribution around the Flower Garden Banks National Marine

Sanctuary is 16-90 m (pers. comm. Flower Garden Banks National Marine Sanctuary public comments to Jennifer Moore, email dated 02/02/21).

Unpublished NCRMP monitoring data indicate the percentage of randomly surveyed sites where *O. faveolata* was present was approximately 30-45% in the US Virgin Islands and Puerto Rico between 2014 and 2019 (Appendix 2, Figure 89). The percentage of sites with *O. faveolata* was stable for Puerto Rico and St. Croix during this period but decreased slightly in St. Thomas/St. John. In the Florida Keys and Dry Tortugas, the percentage of sites with *O. faveolata* present was highly variable between 2014 and 2020, ranging from 25% to 60% in the Dry Tortugas and from 35% to 80% in the Florida Keys with no obvious indication of declining trends overall for either location (Appendix 2, Figure 89). In southeast Florida, the percentage of sites with *O. faveolata* was highest in 2014 at about 20%, decreased to a low of <5% in 2016, then increased and stabilized to about 10% from 2017 to 2020 (Appendix 2, Figure 89).

2.3.5.1.5 Habitat or ecosystem conditions (e.g., amount, distribution, and suitability of the habitat or ecosystem):

There have been new studies examining habitat conditions that are conducive to settlement of *O. faveolata* larvae. In a study of ten species of red algae, including eight species of crustose coralline algae, five species induced settlement; the species that induced the highest settlement and metamorphosis of *O. faveolata* tended to be rare on Belizean reefs and primarily found in low-light environments (Ritson-Williams et al. 2014). A study examining the effects of soundscape on settlement of *O. faveolata* larvae found that settlement chambers with the loudest sounds had significantly higher settlement than those with the quietest sounds, supporting the idea that soundscapes can influence coral recruitment patterns and influence recolonization of degraded sites (Lillis et al. 2016).

2.3.5.2 Five-Factor Analysis (threats, conservation measures, and regulatory mechanisms)

2.3.5.2.1 Present or threatened destruction, modification or curtailment of its habitat or range:

Loss of recruitment habitat continues to be a threat to Caribbean corals, including *O. faveolata*. The presence of algae can inhibit settlement of coral larvae, and in many locations in the Caribbean, there has been a shift from coral dominated to algal dominated reefs partially attributed to the loss of herbivores, including the Caribbean-wide die-off of the long spined sea urchin *D. antillarum* and the trophic effects of over-fishing. There is no new information about the magnitude of this threat to *O. faveolata*.

2.3.5.2.2 Overutilization for commercial, recreational, scientific, or educational purposes:

Although *O. faveolata* is susceptible to collection and trade, it is a low threat that did not contribute to its status. No new information indicates a change in the magnitude of this threat.

2.3.5.2.3 Disease or predation:

Disease

Since the listing, the new SCTLD has emerged impacting at least 24 Caribbean coral species, including five of the seven ESA-listed species (Florida Coral Disease Response Research & Epidemiology Team 2018). It was first observed in Miami, Florida in 2014 and then spread throughout the Florida reef tract over the next several years (Neely 2018; Precht et al. 2016). It has continued to spread throughout much of the Caribbean and has been observed along the Mesoamerican Reef, Bahamas, Greater Antilles, and as far south as St. Lucia in the Lesser Antilles (see https://www.agrra.org/coral-disease-outbreak/ for a map of confirmed sightings of SCTLD in the greater Caribbean). The disease is unprecedented in the temporal and geographic scope as well as the number of susceptible species, prevalence, and rates of mortality (Neely 2018; Precht et al. 2016). In almost all affected species, tissue loss occurs rapidly and leads to full colony mortality. The disease appears to be both water-born and transmissible through direct contact (Neely 2018).

Orbicella faveolata is described as intermediately susceptible to SCTLD since it is not one of the first species to show signs of disease once SCTLD infects a site (Florida Coral Disease Response Research & Epidemiology Team 2018). In surveys of 14 sites off southeast Florida between 2013 and 2015, the prevalence of SCTLD was 13% of *O. faveolata* colonies (Precht et al. 2016). Because almost all colonies succumb completely to SCTLD, prevalence is a good indicator of mortality rate (Precht et al. 2016). In surveys in southeast Florida after Hurricane Irma in 2017, prevalence of disease was 21% of *O. faveolata* colonies, and disease impacted 11% (243 out of 2,130) of sites surveyed (Walker 2018). In surveys along 82 sites in Mexico, prevalence of SCTLD was about 15% for *O. faveolata* (Alvarez-Filip et al. 2019), and in the Bahamas, prevalence of SCTLD was 8% of *O. faveolata* colonies at Grand Bahama and 3% at New Providence (Dahlgren et al. 2021). In the US Virgin Islands long-term monitoring transects, overall initial prevalence of SCTLD in *O. faveolata*/*O. franksi* was about 12% when disease was first reported at a site (Brandt et al. 2021). However, over subsequent surveys, prevalence rose as high as about 45%, reducing the abundance of *O. faveolata*/*O. franksi* colonies from 684 colonies present in the transects between 2005 and 2018 before SCTLD arrived, to just 12 colonies by the end of the study (Brandt et al. 2021).

Topical treatments of antibiotics (amoxicillin) using two different pastes were tested for their effectiveness in treating SCTLD. The pastes in the absence of antibiotics were minimally effective (4% and 9%) at treating disease, but the effectiveness increased dramatically with the addition of the antibiotics (Neely et al. 2020b). Success rate was 90% for *O. faveolata*, indicating the antibiotic paste treatment is a successful method of stopping progression of SCTLD lesions on corals (Neely et al. 2020b).

In addition to SCTLD, several other diseases impact *O. faveolata*, and there have been some new studies examining the causes, effects, and treatments. In a study examining the bacterial assemblages of colonies of *O. franksi* and *O. faveolata*, colonies displaying signs of white plague disease had different abundances of operational taxonomic units of bacteria in healthy versus diseased colonies but not between species, and bacterial richness increased in diseased samples (Roder et al. 2014). In another study, *O. faveolata* colonies with white plague disease exhibited changes in host, symbiont, and micro-organism responses in comparison to healthy colonies (Daniels et al. 2015). Gene expression changes of the coral host included proteins involved with immunity, cytoskeletal integrity, cell adhesion, oxidative stress, and chemical defense. Similarly, bacterial communities exhibited increased heat shock proteins and genes related to oxidative stress and DNA repair. Algal symbionts showed changes in genes related to stress, photosynthesis, and metal transport. Thus, white plague disease resulted in changes in the whole coral holobiont. Additionally, multiple families of bacteria contributed to the changes in gene expression, lending support to the notion that white plague disease is an opportunistic poly-microbial disease. Data also indicated that viruses and phages may play a role in white plague disease (Daniels et al. 2015).

There have been several studies on yellow band disease in *O. faveolata*. In one study, there was a distinct community structure of bacteria in yellow band diseased tissue, apparently healthy tissue on diseased colonies, and healthy colonies (Closek et al. 2014). Bacteria diversity was two to three times higher in diseased tissue, and apparently healthy tissue on diseased colonies had the highest bacterial richness, including components associated with both healthy colonies and diseased tissue, as well as unique bacterial families. Host coral gene expression in diseased tissue exhibited reduced expression of genes associated with defense and metabolism, and apparently healthy tissue had an intermediate expression profile. The authors concluded that although apparently healthy tissue on disease colonies did not show visible signs of disease, they should be considered as an additional intermediate state given the differences in microbial communities and gene expression of the host coral (Closek et al. 2014). Another study, aimed at diagnosing yellow band disease in *O. faveolata* colonies, identified the expression of three genes of interest that could be used to detect the presence of yellow band disease in *O. faveolata* (Morgan et al. 2015). A third study examined three techniques (shading, aspirating, and chiseling a "firebreak" around the lesion) to test for effectiveness of stopping the progression of Caribbean yellow band disease in *O. faveolata* (Randall et al. 2018). The only method that effectively reduced tissue loss was the firebreak, reducing tissue loss by 31%. However, the long-term effectiveness of this method was questionable as success significantly decreased over 23 months despite 30-40% of firebreaks being free of disease 12-16 months after treatment (Randall et al. 2018).

Finally, there were new studies examining the interplay of disease and other stressors. A study examining the effects of hydrocarbon pollution on healthy and diseased colonies of *O. faveolata* found reduced enzymatic activity in colonies infected with yellow band disease, suggesting that *O. faveolata* colonies infected with yellow band disease may be more vulnerable to the effects of chemical pollution (Montilla et al. 2016). In a different study, the progression of black band disease was found to decrease in *O. faveolata* colonies exposed to low pH (7.7) conditions (Muller et al. 2017). Low pH lowered the relative abundance of the bacterial community associated with black band disease, indicating that as oceanic pH decreases with climate change, it may decrease the virulence of black band disease (Muller et al. 2017).

Predation

Orbicella faveolata has low susceptibility to predation, and there is no new information related to this threat.

2.3.5.2.4 Inadequacy of existing regulatory mechanisms:

The threats related to global climate change, including bleaching from ocean warming, ocean acidification, and increased disease (Maynard et al. 2015), pose the greatest potential extinction risk to corals and in the last review were evaluated with sufficient certainty out to the year 2100. We relied on information in the Intergovernmental Panel on Climate Change (IPCC) Fifth Assessment Report (AR5), Climate Change 2013: The Physical Science Basis (IPCC 2013), commonly referred to as the Working Group I Report (WGI). This report presented four Representative Concentration Pathways (RCPs) to simulate future climate change, and we evaluated extinction risk using RCP8.5 which represented the high emissions pathway we were currently on.

The IPCC is now in its sixth assessment cycle (AR6) and has released the WGI report Climate Change 2021: The Physical Science Basis (IPCC 2021) that addresses the most updated physical understanding of the climate system and climate change. The latest report indicates that greenhouse gases have continued to increase in the atmosphere since the 2011 measurements reported in AR5. Strong warming has been observed since 2012, and 2016–2020 was the hottest five-year period recorded since at least 1850. Global surface temperature was 1.09°C higher in 2011–2020 than in 1850–1900. On the current emissions trajectory (RCP8.5), the onset of annual severe coral bleaching in the Caribbean is predicted to occur in 2040-2043 with some regional variation (van Hooidonk et al. 2015); under RCP4.5, which represents lower emissions mid-century than will occur if pledges made following the 2015 Paris Climate Change Conference (COP21) become reality, annual coral bleaching is predicted to occur 11 years later, thus doing little to give corals more time to adapt and acclimate (van Hooidonk et al. 2016). Therefore, existing regulatory mechanisms have continued to be inadequate to protect against climate change and the threat it poses to corals due to ocean warming, ocean acidification, and related increases in disease.

AR6 considers 5 greenhouse gas scenarios: very low (SSP1-1.9), low (SSP1-2.6), intermediate (SSP2-4.5), high (SSP3-7.0), and very high (SSP5-8.5). The report indicates that global surface temperature will continue to increase until at least 2050 under all five emission scenarios considered in the report. Crossing the 2°C global warming level in the period 2041–2060 is "very likely" to occur under the very high emissions scenario (SSP5-8.5), "likely" to occur under the high emissions scenario (SSP3-7.0), and "more likely than not" to occur in the intermediate emissions scenario (SSP2-4.5). In the nearer term (2021-2040), the 1.5°C global warming level is "very likely" to be exceeded under the very high GHG emissions scenario (SSP5-8.5), "likely" to be exceeded under the intermediate and high emissions scenarios (SSP2-4.5 and SSP3-7.0), "more likely than not" to be exceeded under the low emissions scenario (SSP1-2.6) and "more likely than not" to be reached under the very low emissions scenario (SSP1-1.9). With additional global warming, there is high confidence that the frequency of marine heatwaves will continue to increase, particularly in the tropical ocean. There is "likely" to be a global increase in marine heatwaves of 2–9 times in 2081–2100 compared to 1995–2014 under the low emissions scenario (SP1-2.6) and 3–15 times under the very high emissions scenario (SSP5-8.5). Thus, projected warming is expected to increase in the future.

2.3.5.2.5 Other natural or manmade factors affecting its continued existence:

Ocean Warming

Ocean warming continues to be an overarching threat to *O. faveolata*, and there have been some recent studies examining the effects of bleaching on the species and species complex (*O. annularis*, *O. faveolata*, and *O. franksi*). Long-term monitoring of 16 permanent monitoring sites in Puerto Rico showed that the 2005 bleaching event resulted in extreme reductions in coral cover of the species complex; *Orbicella* spp. ranged from approximately 9% to 25% cover before the bleaching event to approximately <2% to 7% up to 10 years after the event (Garcia-Sais et al. 2017). At some sites, partial recovery of coral cover was observed by 2015 but not to the levels observed prior to bleaching. Some sites even experienced a loss in dominance of the species complex (Garcia-Sais et al. 2017).

Historical growth records (1963-2015) of *O. faveolata* were examined in Colombia using coral cores (Lizcano-Sandoval et al. 2019). There was a significant negative correlation of both density and calcification with temperature. Mass bleaching events in 1998, 2005, and 2010 were associated with between year variations in density and calcification by up to 25% relative to the historical mean (Lizcano-Sandoval et al. 2019).

Calcification and growth of *O. faveolata* were examined from 2004 to 2013 at an inshore and offshore reef in the Florida Keys (Manzello et al. 2015). The period encompassed the 2005 Caribbean-wide bleaching event, a cold water event in 2009-2010, and a localized warm water bleaching event in 2011. Growth and calcification rates were higher at the inshore site every year with the exception of years when thermal stress events occurred that only impacted inshore reefs (2009-2010 cold water event and 2011 bleaching event). Coral growth rates inshore recovered quickly from these stress events, and this recovery, in combination with higher calcification rates, likely contributed to the higher coral cover at inshore reefs in the Florida Keys (Manzello et al. 2015).

Another study looked at the long-term effects of bleaching on *O. annularis*, *O. faveolata*, and *O. franksi* reproduction. After bleaching events that occurred in Panama in 2005 and 2010, reduced spawning was observed in all species and persisted for several years (Levitan et al. 2014). Both bleached and unbleached colonies had reduced probability of spawning for several years following the 2010 bleaching event, even though bleaching did not alter coral survival or tissue loss. However, bleached colonies were less likely to spawn than those that did not visibly bleach. The authors concluded that corals that recover from bleaching events can experience a long-term reduction in reproduction over time scales that can bridge the interval between subsequent bleaching events (Levitan et al. 2014).

A study was conducted to test the effects of warming and acidification at levels predicted to occur in 2050 on the fertilization, larval survival, and settlement of *O. faveolata* (Pitts et al. 2020). Warming, acidification, and their combination did not affect fertilization, but warming caused complete larval mortality and thus prevented any settlement. However, larval survival and settlement under the combined treatment of warming and acidification was higher than in the warming treatment alone, indicating a modulating effect of lower pH on increased larval metabolism under warming conditions. Larval survival and settlement were decreased by 50% compared to control conditions, indicating predicted warming and acidification due to climate change will negatively impact early life stages of *O. faveolata* (Pitts et al. 2020).

In a laboratory study examining symbiont shuffling in *O. faveolata* in response to bleaching, changes in zooxanthellae communities depended on initial symbiont community composition, the severity of disturbance, and the recovery temperature (Cunning et al. 2015). *Orbicella faveolata* colonies that experienced more extreme bleaching had a larger increase in the proportion of heat-tolerant zooxanthellae during recovery, particularly those that recovered in warmer conditions, than those that bleached mildly. Higher proportions of heat-tolerant zooxanthellae increased bleaching resistance but also reduced photochemical efficiency, indicating trade-offs in bleaching resistance and physiological performance (Cunning et al. 2015).

In a laboratory study to examine the effects of annual bleaching on thermal tolerance, the phenotypic plasticity in the dominant algal symbiont of *O. faveolata* did not prevent repeat bleaching in the second year (Grottoli et al. 2014). However, it may have contributed to rapid recovery. The authors postulated this rapid recovery may lead to the potential ability of this species to acclimatize and persist with predicted increased frequency of bleaching events as a result of climate change (Grottoli et al. 2014).

A study at ten sites in the Florida Keys sampled *O. faveolata* colonies during the 2015 bleaching event and 8 months later to determine bleaching levels and symbiont types (Manzello et al. 2019). The colonies at the inshore sites had higher bleaching resistance and better recovery than those at offshore sites, despite having been exposed to higher temperatures. The thermally tolerant symbiont *Durusdinium trenchii* was dominant region-wide, and greater than 90% of the non-bleached corals were dominated by this symbiont. Previous studies rarely found *D. trenchii* as the dominant symbiont in *O. faveolata* colonies in the Florida Keys, and it is likely the high abundance found in this study was a result of back-to-back bleaching events in 2014 and 2015 (Manzello et al. 2019).

Similarly, a field study that followed *O. faveolata* colonies in the Florida Keys before, during, and after bleaching events in 2014 and 2015 found that there was less bleaching in 2015 despite longer time spent above the local bleaching temperature threshold (Fisch et al. 2019). Approximately 75% of colonies bleached less than or the same amount as in 2014 with a minority of approximately 35% faring better in the second event. Although there appeared to be some acclimation response to the second bleaching event, lipid levels in the colonies did not return to pre-bleaching levels, indicating reduced energy storage due to repeated bleaching. Colonies that bleached more severely in 2014 were less likely to spawn the following year and released a lower proportion of gametes (gametes released from <50% of the colony surface area). Lipid levels and symbiont-to-host cell ratios at the bottom edge of the colony during the recovery period were most predictive of likelihood of spawning the next year (Fisch et al. 2019).

A study was undertaken to examine the effects of feeding on the response of *O. faveolata* colonies to elevated temperatures and CO_2 mimicking predicted conditions due to climate change (Towle et al. 2017). Feeding corals enhanced their physiology under stress. Growth was highly correlated to the source location of the colonies, and growth, symbiont density, chlorophyll a content, and lipid content were positively correlated to feeding. Calcification was depressed in the presence of elevated CO_2 and in the absence of feeding (Towle et al. 2017).

A study of two sites in the Bahamas that had differential bleaching response to a warm-water event found that the site that did not bleach was comprised of multiple colonies of a single *O. faveolata* genotype that exclusively hosted *Durusdinium* symbionts (Parker et al. 2020). The colonies at the non-bleached site also had a higher species richness of bacterial families. The study supports the notion that while increased temperatures due to climate change will likely greatly reduce genetic diversity, conditions at some sites may select for heat-tolerant genotypes of coral and symbionts that may be able to persist (Parker et al. 2020).

Finally, a study in Panama examined the potential for heritability of variation in bleaching response of *O. faveolata* colonies to warmer temperatures using stress experiments and relatedness of genotypes determined through single nucleotide polymorphism (SNP) analysis (Dziedzic et al. 2019). It found that the variation in response was highly heritable, suggesting the potential for adaptive response of *O. faveolata* to warming in this region.

Acidification

There have been new studies on the effects of elevated CO_2 and acidification on growth and calcification of *O. faveolata*. In a study of historical growth records (1963-2015) of cores of *O. faveolata* in Colombia, density and calcification showed a significant reduction over time, which was best explained by changes in aragonite saturation (Lizcano-Sandoval et al. 2019). In a study of calcification of several species of Caribbean corals under conditions of elevated temperature and pCO_2, *O. faveolata* had reduced calcification in both elevated temperature and pCO_2 conditions during 2 months of exposure (Okazaki et al. 2017). In a fully crossed factorial experimental design, *O. faveolata* hosting *Symbiodinium* D were exposed to combinations of a normal (26°C) and elevated (32°C) temperature and normal (380 ppm) and elevated (800 ppm) CO_2 for 62 days and then recovered at 26°C or 32°C and normal CO_2 for an additional 56 days (Langdon et al. 2018). CO_2 enrichment did not confer enhanced thermal tolerance as had been suggested in other studies, and *O. faveolata* colonies exposed to high CO_2 experienced a 47% reduction in growth. The authors concluded that *O. faveolata* with D symbionts might survive to 2060 and later but its abundance will be impacted by CO_2 effects on recruitment potential (Langdon et al. 2018).

Sedimentation

A study examined the effects of algal turfs and algal turfs plus sediment on settlement of *O. faveolata*. It found that the presence of turf algae (1.8–5.2mm canopy height) alone did not reduce settlement, but the presence of naturally accumulating sediment (1-3 mm) reduces settlement 13-fold compared to turf algae alone (Speare et al. 2019). This result was corroborated by field surveys in the Florida Keys that showed a strong negative relationship between the abundance of turf algae plus sediment (mean sediment depth of 4.6 mm; range 2-7 mm) and the abundance of juvenile corals (Speare et al. 2019).

Nutrients

There have been new studies on the effects of contaminants and nutrients on *O. faveolata*. Colonies of *O. faveolata* exposed to nanoparticles of titanium dioxide exhibited a stress response after exposure to the contaminant for 17 days (Jovanovic and Guzman 2014). All colonies expelled zooxanthellae and expressed the gene for heat shock proteins, but no mortality occurred (Jovanovic and Guzman 2014). In a study examining the effects of elevated dissolved inorganic nitrogen and/or increased temperature on oxygen consumption in larval *O. faveolata*, larvae increased respiration in response to elevated temperature but not to nitrate enrichment (Serrano et al. 2018). The effects of elevated temperature and nitrate enrichment were neither additive nor synergistic (Serrano et al. 2018).

An experiment was conducted to test the effects of increased (sub-bleaching) temperature and excess nitrogen on the symbiotic relationship of *O. faveolata* and *Symbiodinium* (Baker et al. 2018). Warming to 31°C in the presence of elevated nitrate reduced the net primary productivity of the holobiont by 60%, resulting in a 15% decrease in carbon to the coral host and no apparent cost to the symbionts. *Symbiodinium* carbon and nitrogen assimilation increased by 14% and 32%, respectively, and the mitotic index increased by 15%, without a proportional gain in translocated photosynthates to the coral host. The authors concluded that warming temperature in combination with excess nutrients benefits the symbiont without a concurrent benefit to the coral host, indicating symbiont parasitism of the coral symbiosis (Baker et al. 2018).

A study examining the effects of symbionts on the immunity of *O. faveolata* found that increases in symbiont density resulting from nutrient enrichment elicited a negative effect on host expression of immune-related transcripts (Fuess et al. 2020). The authors postulated that links between nutrient enrichment and coral disease may be the result of increased symbiont density that suppresses the immune response of corals rather than a direct effect of the nutrients themselves (Fuess et al. 2020).

Conservation Measures

Coral propagation for use in conservation and restoration has expanded to include more of the slower-growing mounding corals such as *O. faveolata*. Micro-fragmenting of corals and attaching the pieces to hard surfaces in close proximity has been shown to be a successful way of rapidly increasing colony size through subsequent faster growth and fusion. However, fish predation on the micro-fragments after placement on the reef can sometimes be an issue. In one experiment, micro-fragmented *O. faveolata* colonies grew as much as 63 cm^2 per month, which was faster than two other non-ESA listed species tested (Forsman et al. 2015). There was a relationship between initial size of fragments and growth with larger fragments growing faster (Forsman et al. 2015). However, in a field experiment, micro-fragmented *O. faveolata* colonies (1 cm^2) produced tissue 6.5 times higher than larger fragments (16-64 cm^2) when samples with more than 40% predation were removed from the analysis (Page et al. 2018). Initial predation occurred on the micro-fragments and not the larger fragments, but growth and survival did not differ between the groups after 31 months (Page et al. 2018).

Several experiments were undertaken to understand and limit the effects of predation on *O. faveolata* outplants for restoration. Larger colonies (25 cm^2) were less susceptible to predation than smaller colonies (5 cm^2), and some genotypes were more susceptible than others (Rivas 2020). There was evidence that predation was likely driven by consumption of corals and not territorial behavior of fish (Rivas 2020). Therefore, the author concluded that restoration success can be improved if larger *O. faveolata* colonies of multiple genotypes are outplanted near larger, complex colonies that limit fish access (Rivas 2020).

Finally, a study tested the efficacy of cryopreserving *O. faveolata* sperm for use in larval propagation and restoration. Fresh sperm were still motile and viable for more than 5 hours after release from gamete bundles (Vanegas and Pizarro 2018). When thawed, cryopreserved *O. faveolata* sperm showed no difference in sperm motility, morphology, or viability compared to fresh sperm (Vanegas and Pizarro 2018). Thus, cryopreservation may be a useful tool for sexual propagation and restoration of *O. faveolata*.

2.3.5.3 Synthesis

At the time of listing as threatened (in danger of extinction within the foreseeable future), *O. faveolata*'s common occurrence, distribution, and life history strategy, in which large, long-lived colonies were able to buffer losses and allow the species to persist despite slow growth and extremely low recruitment, were determined to moderate the species' vulnerability to extinction. It was expected that this buffering capacity would decrease with declining populations as threats were predicted to increase into the future. It was not considered as endangered (currently in danger of extinction) at the time of listing because its population was abundant and not so low or fragmented to indicate depensatory processes were in effect and because exposure to threats was moderated by its inhabitation of multiple habitats across a wide depth range, including shallow and mesophotic depths, that would experience highly variable thermal regimes at local and regional scales.

New information published on *O. faveolata* population abundance confirms that it was relatively common and abundant in most locations surveyed prior to 2014 when the species was listed as threatened. In surveys conducted since the listing, *O. faveolata* was still relatively common and present at a large percentage of sites in Florida, Puerto Rico, and the US Virgin Islands. However, in some locations around Cuba, *O. faveolata* was uncommon, indicating declines. Although it can occur at deeper depths, *O. faveolata* has not been observed in mesophotic areas of the Florida Keys, Dry Tortugas, or Pulley Ridge in the Gulf of Mexico. It has been observed on additional banks near the Flower Gardens in the Gulf of Mexico. Since the listing, live cover and average colony size of *O. faveolata* have decreased in some areas such as the Florida Keys and southeast Florida but have remained more stable in others such as the US Virgin Islands, Puerto Rico, and the Dry Tortugas. Partial colony mortality has increased in Florida while remaining lower and more stable in the US Virgin Islands and Puerto Rico. Density has remained relatively stable in most locations surveyed. All of the new information suggests that *O. faveolata* has had mixed population trends with some decline and some stability.

New genetic information indicates there is likely an eastern and western population with substructure at local and regional scales. Genetic diversity seems to be high across the range. There is some new evidence to suggest clonality in *O. faveolata* may be higher than expected in some individual sites. Additionally, one study found low reproductive compatibility between genotypes, indicating the effective population size may be lower than the standing population.

At the time of listing, *O. faveolata* was described as highly susceptible to ocean warming as evidenced by high bleaching prevalence, negative effects on larval development and survival, and lowered growth and calcification for several years after bleaching. New studies since the listing have confirmed decreased larval survival and calcification of *O. faveolata* with warmer temperatures, as well as lower growth and skeletal density. In addition, new information suggests that warming temperatures can lower *O. faveolata* spawning for several years after anomalously high water temperature and bleaching. Reduced spawning may be a result of depleted energy reserves, and lab studies indicate that energy reserves may be augmented by heterotrophic feeding. There is new evidence that symbiont shuffling can occur during bleaching events that can confer some resistance to subsequent bleaching and/or faster recovery. However, there are likely trade-offs in symbiont bleaching resistance and coral performance. Finally, variation in heat tolerance of *O. faveolata* appears to be heritable, suggesting the potential for an adaptive response of *O. faveolata* for genotypes that are able to survive warming temperatures. All of the new information confirms that *O. faveolata* is highly susceptible to ocean warming.

Orbicella faveolata was described as highly susceptible to disease at the time of listing. New studies have examined the causes, effects, and treatment of diseases including white plague disease and yellow band disease, as well as the interaction of disease with other stressors, such as acidification and hydrocarbon pollution. Since the listing, SCTLD has emerged as a new disease that has had a large impact on many coral species. *Orbicella faveolata* has been described as intermediately susceptible to SCTLD based on the observation that it is not one of the first species to contract the disease once it appears at a site. Prevalence of SCTLD in *O. faveolata* has been observed as low as 3% to as high as 45% and can increase over time as has been observed in the US Virgin Islands. Because total colony mortality often results from SCTLD and because SCTLD has been progressing to new sites around the Caribbean without signs of slowing or seasonality, both the scope and severity of disease have increased in relation to the threat they pose to *O. faveolata* since the time of listing.

In the listing determination, *O. faveolata* was described as highly susceptible to acidification due to reduced fertilization and growth of colonies. Since the listing, new studies have shown that *O. faveolata* exposed to conditions of increased pCO_2 or reduced aragonite saturation have experienced decreased skeletal density, calcification, and growth. Thus, new studies support the determination that *O. faveolata* is highly susceptible to acidification.

When *O. faveolata* was listed, it was categorized as highly susceptible to sediments. Since the listing, there has been new information that accumulated sediment (1-3 mm) in the presence of turf algae reduces the settlement of *O. faveolata*. This information supports the description of *O. faveolata* as highly susceptible to sediments.

Oribicella faveolata was also described as highly susceptible to nutrients in the listing rule. New studies have examined the role of nutrient enrichment on the symbiotic relationship of *O. faveolata* and zooxanthellae. In the presence of increased temperatures, excess nitrogen resulted in an increase in symbiont density without a proportional gain in food for the coral host, indicating symbiont parasitism of the coral symbiosis. Increases in symbiont density resulting from nutrient enrichment was also shown to suppress the immune response of *O. faveolata*, potentially making it more susceptible to disease. These findings provide further support that *O. faveolata* is highly susceptible to nutrients.

The susceptibility of *O. faveolata* to other threats identified at the time of listing include some susceptibility to the trophic effects of fishing and low susceptibility to predation and collection and trade. There is no new species-specific information about these threats.

In summary, although populations of *O. faveolata* and the buffering capacity of its life history strategy continue to decrease in some areas, the species has had stable population trends since the listing in other locations. It still inhabits its historical range and maintains its historical distribution. It appears to remain relatively common in most locations where information is available, and there is no indication that its populations are so low or fragmented that depensatory processes are affecting the species. The susceptibility of *O. faveolata* to threats identified at the time of listing has not changed, though the emergence of SCTLD has increased the vulnerability of *O. faveolata* to disease. Based on all these factors, *O. faveolata* continues to be at risk of extinction in the foreseeable future but does not appear to be currently at risk of extinction. Thus, no change in status is recommended at this time.

2.3.6 DENDROGYRA CYLINDRUS

2.3.6.1 Biology and Habitat

2.3.6.1.1 New information on the species' biology and life history:

There have been new studies on reproductive life history of *D. cylindrus*. The species has been observed to spawn on nights 2-5 after the full moon in August and September in Curaçao (Marhaver et al. 2015) and on nights 2-4 after the full moon in July and August in Florida (Neely et al. 2020a). Colonies spawned over multiple nights, and males began spawning on average 6.5 to 13 minutes before females (Neely et al. 2020a). Based on the observation of female colonies that exposed their eggs to ambient seawater through slits near their mouths, it is possible that eggs are fertilized within female colonies prior to release (Marhaver et al. 2015). Colonies held outdoors within *ex situ* facilities exposed to ambient light had more variable and less predictable spawning, which the authors attributed to exposure to light pollution that interfered with signaling; spawning occurred later after sunset and across more nights (Neely et al. 2020a). When colonies were held indoors in induced spawning systems set to mimic natural light and temperature conditions observed on the reef, spawning was more predictable and occurred within the timeframes observed in the wild (O'Neil et al. 2021).

Dendrogyra cylindrus was previously classified as gonochoric, but evidence of hermaphroditism has been observed both in histological samples from Florida (Kabay 2016) and from spawning observations in the Florida Keys over several seasons (Neely et al. 2018; Neely et al. 2020a). Histological samples from the upper Florida Keys and southeast Florida revealed that hermaphrodites produced eggs and sperm within the same sample, within the same polyp, and within the same mesentery (Kabay 2016). Hermaphrodites from sites in southeast Florida and one site in the Florida Keys produced predominantly male gametes (60-80%). The other site in the Florida Keys only had one hermaphroditic colony in which 99% of gametes were oocytes, and all other colonies sampled at this site were female (Kabay 2016). In spawning observations, colonies that were previously observed to be either male or female changed to hermaphrodites in subsequent years, and one colony changed from hermaphrodite to male (Neely et al. 2018). Also, separate colonies of the same genotype produced either male or female gametes, and 22% of the observed ramets produced both eggs and sperm within separate regions of the same colony (Neely et al. 2018). At least 35% of the genotypes observed (n=29) in the Florida Keys have shown signs of hermaphroditism (Neely et al. 2020a). Of the 29 genotypes, one spawned both eggs and sperm simultaneously over 3 consecutive years, seven spawned as different genders on different nights of the same year, and 8 spawned as different genders in different years (Neely et al. 2020a). This flexibility in reproductive mode may be a strategy to improve the chances of successful reproduction for a species that is naturally rare and whose potential mates are scarce (Neely et al. 2018).

There is also new but limited information on larval development and symbionts in *D. cylindrus*. In fertilization experiments, larvae developed rapidly, becoming fully developed in less than 16 hours after fertilization, and settlement was first observed 4 days after spawning (Marhaver et al. 2015). *Dendrogyra cylindrus* hosts multiple species of symbioints, but it forms an obligate symbiosis with the rare species, *Breviolum* (formerly *Symbiodinium* Clade B) *dendrogyrum*, which has only been observed in *D. cylindrus* (Lewis et al. 2019a).

2.3.6.1.2 Abundance, population trends (e.g. increasing, decreasing, stable), demographic features (e.g., age structure, sex ratio, family size, birth rate, age at mortality, mortality rate, etc.), or demographic trends:

Dendrogyra cylindrus has been described as a naturally rare species, and population status and trends have been difficult to discern due to low encounter rates. The results of demographic modeling based on molecular data did not reveal evidence of past changes in *D. cylindrus* population size, which agrees with the geologic record that this species has always been rare (Chan et al. 2019).

Unpublished NCRMP monitoring data from stratified random sites (different site surveyed each year) show a decrease in the percent cover of *D. cylindrus* in Puerto Rico and the US Virgin Islands after 2016/2017 (Appendix 2, Figure 115). Density of colonies generally follows the same trend except for Puerto Rico where density increased between 2014 and 2019 (Appendix 2, Figure 116). These patterns mimic the pattern of the percentage of sites with *D. cylindrus* present (Appendix 2, Figure 118).

Surveys of *D. cylindrus* were conducted in 2002 and again in 2012 in Old Providence and St. Catalina Islands, which host more than 90% of the *D. cylindrus* population in Colombia (Bernal-Sotelo et al. 2019). The surveys revealed that 3 of the 4 occupied habitats (defined by the area of reef where *D. cylindrus* was present) used by the species in 2002 were present in 2012 but reduced in area. Half of the 60 m diameter radial plots that contained more than 4 colonies of *D. cylindrus* in 2002 contained no living colonies of *D. cylindrus* 10 years later. The number of colonies observed in 2002 was 213 versus 261 colonies in 2012; the number of fragments was 70 in 2002 versus 585 fragments observed in 2012, and almost 97% of the fragments observed in 2012 were produced as a result of partial colony mortality. Average colony and fragment size was smaller in more recent surveys, and the number of colonies with partial mortality and the amount of partial mortality were also higher. Larger colonies (≥115 cm) had higher partial and total mortality. The authors concluded that the reduced amount of living tissue, dominance of asexually produced fragments, and smaller fragment size limit the potential for population growth, making this population very vulnerable and at risk of local extinction (Bernal-Sotelo et al. 2019).

Demographic modeling of *D. cylindrus* was conducted for Florida using different survival scenarios of 80, 50, and 20 percent of the population after the 2014/2015 thermally-induced disease outbreaks and assuming no sexual reproduction, no establishment of asexual recruits, and no successful restoration (Chan et al. 2019). The number of stress events before local extinction occurred was 31 for the 80% survival scenario, 11 for the 50% survival scenario, and 6 for the 20% survival scenario (Chan et al. 2019). Assuming two stress events per decade until 2042 when thermal stress events are predicted to become annual, local extinction of *D. cylindrus* in Florida was modeled to occur in 2066 for the 80% survival scenario, and in 2046 and 2039 for 50% survival and 20% survival, respectively (Chan et al. 2019). However, as described later in this section, the emergence of SCTLD resulted in local extinction occurring sooner than predicted in these modeling scenarios. In a separate field study of the same region and the same 2014/2015 bleaching events, recovery from bleaching in Florida was calculated to take 11 years (in the absence of severe stressors) based on colony growth rates (~4% annual increase in live tissue) observed after bleaching but before SCTLD affected the colonies (Neely et al. 2021).

In 2014, there were 610 known colonies of *D. cylindrus* at 110 locations along the Florida reef tract, and of these, 65 colonies occurred in southeast Florida across 23 locations (Kabay 2016). About half of the sites contained a single colony, and the most colonies at a site was 14. A severe disease outbreak occurred in Florida following the 2014 and 2015 bleaching events, resulting in a 96% decrease in live tissue and mortality of 86% of the known colonies in southeast Florida during the two years of monitoring. This disease outbreak was later identified as SCTLD. Bleaching was present in 49% of colonies in

2014 and 33% in 2015. Disease was present in 18% of colonies in May 2014, increasing to 47% by September 2015. In April 2016, 100% of the remaining live *D. cylindrus* colonies in southeast Florida had active disease margins. Mean percent live tissue decreased from 84% in May 2014 to 3% in April 2016 (Kabay 2016).

All known colonies in the Florida population of *D. cylindrus* were fate tracked from 2014 to 2020 (Neely et al. 2021). Monitoring included 819 colonies of an assumed 190 genotypes based on colony distances from each other. Over half of the colonies were represented by 5 genotypes, and 62% of the genotypes were represented by a single colony. Asexual reproduction accounted for 77% of the colonies, and distances between genotypes on average was about 1 km, ranging from 2 km to 6.6 km. Average colony diameter and height were 168 cm and 124 cm, respectively, and the largest colony was more than 5 m in length and 3 m in height. During baseline surveys in 2013-2014 (542 colonies, 533 alive), average percent live tissue was 70% (including the dead colonies), and 22% of the colonies exhibited low (2.2%) recent mortality. During the monitoring period, there were chronic stressors, including damselfish gardens/nests, predation by *C. abbreviata*, competition with other benthic organisms, and abrasion and burial, that occurred on about 1% of colonies and caused minor damage (on average ≤1% tissue loss). However, acute stressors, including bleaching events in 2014 and 2015 and an outbreak of SCTLD first identified in *D. cylindrus* as a distinct disease in 2016, resulted in extremely high mortality. By the end of the monitoring period in 2020, there had been a loss of 94% of coral tissue, 93% of colonies, and 86% of genotypes due primarily to disease and bleaching. At the end of 2020, there were 25 known genotypes remaining (out of the 190 genotypes identified), half of which had declined to less than 2% live tissue, and the other half were actively experiencing rapid tissue loss due to SCTLD, though 5 were treated with topical antibiotics to slow or halt the lesions. Only two genotypes remained unaffected and were located in the Dry Tortugas where SCTLD had not yet reached at the time of the study (but has now). The authors conclude that *D. cylindrus* is now functionally extinct along the Florida reef tract (Neely et al. 2021).

2.3.6.1.3 Genetics, genetic variation, or trends in genetic variation (e.g., loss of genetic variation, genetic drift, inbreeding, etc.):

For a study of genetic population and clonal structure, samples of *D. cylindrus* were collected from Florida, Belize, the US Virgin Islands, Curaçao, and the Turks and Caicos (Chan et al. 2019). *Dendrogyra cylindrus* was highly clonal at sites in Florida with multiple colonies present; out of 161 samples across 51 sites, there were 56 unique genotypes, meaning that multiple colonies present at a site were predominantly from asexual reproduction. The typical maximum dispersal distance of asexual fragments was 60 m, though one fragment was found at over 80 m (Chan et al. 2019). The Florida population had low genotypic richness and diversity, and the majority of sites only contained one colony. The highest number of unique genotypes at a site was three, and no sites shared genotypes. Using microsatellite markers, three genetic populations were detected: Florida, Belize, and Turks and Caicos were in one cluster, the US Virgin Islands in another, and Curaçao in a third. There was also evidence of admixing in the Turks and Caicos from both Florida and the US Virgin Islands (Chan et al. 2019).

2.3.6.1.4 Spatial distribution, trends in spatial distribution (e.g. increasingly fragmented, increased numbers of corridors, etc.), or historic range (e.g. corrections to the historical range, change in distribution of the species' within its historic range, etc.):

Dendrogyra cylindrus experienced a decrease in its spatial distribution with the mortality of wild colonies in the northernmost portion of its range in Florida; only two known healthy colonies remained in the Dry Tortugas in 2020, rendering the species functionally extinct in Florida (Neely et al. 2021). In other locations such as Mexico and the US Virgin Islands, local extirpation at specific sites has been reported, rendering the population more fragmented than it was previously (Alvarez-Filip et al. 2019; Brandt et al. 2021).

2.3.6.2 Five-Factor Analysis (threats, conservation measures, and regulatory mechanisms)

2.3.6.2.1 Present or threatened destruction, modification or curtailment of its habitat or range:

Loss of recruitment habitat continues to be a threat to Caribbean corals, including *D. cylindrus*. The presence of algae can inhibit settlement of coral larvae, and in many locations in the Caribbean, there has been a shift from coral dominated to algae dominated reefs partially attributed to the loss of herbivores, including the Caribbean-wide die-off of the long spined sea urchin *D. antillarum* and the trophic effects of over-fishing. In addition, there has been a contraction of the range of *D. cylindrus* with the die-off of colonies in Florida in the northern-most portion of its range.

2.3.6.2.2 Overutilization for commercial, recreational, scientific, or educational purposes:

Although *D. cylindrus* is susceptible to collection and trade, these are low threats that did not contribute to its status. No new information indicates a change in the magnitude of this threat.

2.3.6.2.3 Disease or predation:

Disease

Since the listing, SCTLD has emerged, impacting at least 24 Caribbean coral species, including five of the seven ESA-listed species (Florida Coral Disease Response Research & Epidemiology Team 2018). It was first observed in Miami, Florida in 2014 and then spread throughout the Florida reef tract over the next several years (Neely 2018; Precht et al. 2016). It has continued to spread throughout much of the Caribbean and has been observed along the Mesoamerican Reef, Bahamas, Greater Antilles, and as far south as St. Lucia in the Lesser Antilles (see https://www.agrra.org/coral-disease-outbreak/ for a map of confirmed sightings of SCTLD in the greater Caribbean). The disease is unprecedented in temporal and geographic scope as well as the number of susceptible species, prevalence, and rates of mortality (Neely 2018; Precht et al. 2016). In almost all affected species, tissue loss occurs rapidly and leads to full colony mortality. The disease appears to be both water-born and transmissible through direct contact (Neely 2018). Furthermore, SCTLD does not appear to be seasonal like many other coral diseases that will ramp up during higher temperatures but then decrease as water temperatures cool.

Dendrogyra cylindrus is highly susceptible to SCTLD and is often one of the first species to become infected (Florida Coral Disease Response Research & Epidemiology Team 2018). Between 2014 and 2020, the Florida population of *D. cylindrus* was essentially extirpated by disease, which was later recognized as SCTLD. Surveys of the progression and impact of SCTLD have shown that *D. cylindrus* exhibits high disease prevalence and colony mortality. In the Bahamas, 67% of *D. cylindrus* colonies (n=15) were infected with SCTLD in surveys of Grand Bahama, and 13% of *D. cylindrus* colonies (n=8) were infected in New Providence (Dahlgren et al. 2021). In Mexico, 71% of *D. cylindrus* colonies surveyed (n=7) were infected with SCTLD, and *D. cylindrus* disappeared from several mainland coastal sites (Alvarez-Filip et al. 2019). In addition, the authors noted that colonies of *D. cylindrus* in Cozumel were becoming increasingly infected with SCTLD. In the US Virgin Islands, 1 of 2 *D. cylindrus* colonies (50%) in long-term monitoring transects were infected, but prior to the appearance of SCTLD between 2005 and 2018, there were 11 colonies of *D. cylindrus* in the monitoring transects, indicating high mortality due to SCTLD but not captured in the prevalence data (Brandt et al. 2021). The authors also noted that in surveys of sites affected by SCTLD, numerous recently dead colonies of *D. cylindrus*, presumably from SCTLD, were observed and that it was increasingly rare to find live colonies, even in locations where the species had been relatively abundant.

In monitoring of all known colonies in Florida, several diseases were observed to affect *D. cylindrus* including black band disease, white plague, an unidentified yellow band disease, and SCTLD (Neely et al. 2021). Black band disease was documented for the first time to affect *D. cylindrus* following bleaching events in 2014 and 2015 in the Florida Keys (Lewis et al. 2017). Black band disease was observed on 4.7% of 163 colonies monitored across 28 sites along the Florida reef tract in 2014 and 6.7% of colonies in 2015 (Lewis et al. 2017). Black band disease has rarely been reported to affect *D. cylindrus*, and the authors postulated that the occurrence of the disease in 2014 and 2015 was likely related to the anomalously high temperatures and subsequent bleaching of *D. cylindrus* colonies (Lewis et al. 2017).

Predation

Dendrogyra cylindrus is susceptible to predation from the corallivorous snail *C. abbreviata* and from damselfish gardens and nests. However, these are chronic stressors that generally have low prevalence (~1% of colonies) and result in low amounts (on average ≤1%) of tissue loss (Neely et al. 2021).

2.3.6.2.4 Inadequacy of existing regulatory mechanisms:

The threats related to global climate change, including bleaching from ocean warming, ocean acidification, and increased disease (Maynard et al. 2015), pose the greatest potential extinction risk to corals and in the last review were evaluated with sufficient certainty out to the year 2100. We relied on information in the Intergovernmental Panel on Climate Change (IPCC) Fifth Assessment Report (AR5), Climate Change 2013: The Physical Science Basis (IPCC 2013), commonly referred to as the Working Group I Report (WGI). This report presented four Representative Concentration Pathways (RCPs) to simulate future climate change, and we evaluated extinction risk using RCP8.5 which represented the high emissions pathway we were currently on.

The IPCC is now in its sixth assessment cycle (AR6) and has released the WGI report Climate Change 2021: The Physical Science Basis (IPCC 2021) that addresses the most updated physical understanding of the climate system and climate change. The latest report indicates that greenhouse gases have continued to increase in the atmosphere since the 2011 measurements reported in AR5. Strong warming has been observed since 2012, and 2016–2020 was the hottest five-year period recorded since at least 1850. Global surface temperature was 1.09°C higher in 2011–2020 than in 1850–1900. On the current emissions trajectory (RCP8.5), the onset of annual severe coral bleaching in the Caribbean is predicted to occur in 2040-2043 with some regional variation (van Hooidonk et al. 2015); under RCP4.5, which represents lower emissions mid-century than will occur if pledges made following the 2015 Paris Climate Change Conference (COP21) become reality, annual coral bleaching is predicted to occur 11 years later, thus doing little to give corals more time to adapt and acclimate (van Hooidonk et al. 2016). Therefore, existing regulatory mechanisms have continued to be inadequate to protect against climate change and the threat it poses to corals due to ocean warming, ocean acidification, and related increases in disease.

AR6 considers 5 greenhouse gas scenarios: very low (SSP1-1.9), low (SSP1-2.6), intermediate (SSP2-4.5), high (SSP3-7.0), and very high (SSP5-8.5). The report indicates that global surface temperature will continue to increase until at least 2050 under all five emission scenarios considered in the report. Crossing the 2°C global warming level in the period 2041–2060 is “very likely” to occur under the very high emissions scenario (SSP5-8.5), “likely” to occur under the high emissions scenario (SSP3-7.0), and “more likely than not” to occur in the intermediate emissions scenario (SSP2-4.5). In the nearer term (2021-2040), the 1.5°C global warming level is “very likely” to be exceeded under the very high GHG emissions scenario (SSP5-8.5), “likely*”* to be exceeded under the intermediate and high emissions scenarios (SSP2-4.5 and SSP3-7.0), “more likely than not*”* to be exceeded under the low emissions scenario (SSP1-2.6) and “more likely than not*”* to be reached under the very low emissions scenario (SSP1-1.9). With additional global warming, there is high confidence that the frequency of marine heatwaves will continue to increase, particularly in the tropical ocean. There is “likely” to be a global increase in marine heatwaves of 2–9 times in 2081–2100 compared to 1995–2014 under the low emissions scenario (SP1-2.6) and 3–15 times under the very high emissions scenario (SSP5-8.5). Thus, projected warming is expected to increase in the future.

2.3.6.2.5 Other natural or manmade factors affecting its continued existence:

Ocean Warming

There have been new studies on the effects of ocean warming on *D. cylindrus*. In a study examining calcification rates in male and female colonies of *D. cylindrus*, calcification was negatively related to sea surface temperature in females, but not in males, indicating future warming predicted under climate change may have disparate effects on the different sexes and implications for population dynamics of *D. cylindrus* (Cruz-Ortega et al. 2020). In recurrent bleaching events in 2014 and 2015, when temperature exceeded the local bleaching threshold of 30.5°C for 8 and 11 weeks, respectively, all *D. cylindrus* colonies at 3 sites in the Florida Keys were severely bleached in 2014, but there were differences between sites during the 2015 bleaching event (Lewis et al. 2019b). One site had no bleaching of *D. cylindrus* colonies, and at another, bleaching was less severe than in 2014 despite longer exposure to elevated temperatures in 2015. The third site bleached severely again in 2015. Bleaching resistance was associated with the changing of the symbiont assemblage from the typically dominant and host-specialist *Breviolum dendrogyrum* to the host-generalist *B. meandrinium* that usually occurs at background densities in *D. cylindrus* (Lewis et al. 2019b). This increase in *B. meandrinium* during the first bleaching event and recovery period resulted in bleaching resistance during the second bleaching event, indicating that stress events can result in symbiont shuffling that may impart resilience to changing ocean conditions (Lewis et al. 2019b).

Acidification

At the time of listing, *D. cylindrus* was presumed to be susceptible to ocean acidification. There is no new species specific information related to this threat.

Sedimentation

At the time of listing, *D. cylindrus* was presumed to be susceptible to sedimentation. There is no new species specific information related to this threat.

Nutrients

At the time of listing, *D. cylindrus* was presumed to be susceptible to nutrients. There is no new species specific information related to this threat.

Conservation Measures

There have been efforts to preserve genetic material of *D. cylindrus* in Florida by collecting colonies from the wild and maintaining them in land-based systems. From May 2016 to December 2018, a rescue effort was undertaken to collect fragments of all remaining *D. cylindrus* genotypes left after the severe declines following the 2014/2015 bleaching events and subsequent disease (Kabay 2016; O'Neil et al. 2021). Fragments were brought into both *in situ* and *ex situ* nurseries to preserve the remaining genetic diversity and aid in propagation and future restoration (Kabay 2016; O'Neil et al. 2021). As of the end of 2020, 543 fragments of 123 Florida genotypes of *D. cylindrus* were being held in nurseries for genetic preservation and to be used as broodstock for future restoration (Neely et al. 2021).

There have been several studies examining the feasibility of sexually propagating *D. cylindrus* for use in conservation efforts. *Dendrogyra cylindrus* was successfully sexually propagated in the lab to the primary polyp settler stage through collection and fertilization of gametes in the field (Marhaver et al. 2015). However, initial settlers did not survive long after 7 months and showed no formation of new polyps through budding, indicating more research and work is needed for sexual propagation to be a viable restoration method (Marhaver et al. 2015). Spawning has been observed both in outdoor holding facilities and in indoor induced spawning tanks set to mimic natural environmental light and temperature regimes (Neely et al. 2020a; O'Neil et al. 2021). In an induced spawning system holding 21 *D. cylindrus* genotypes, over 50,000 viable *D. cylindrus* larvae were produced from only a fraction of the spawn that was collected in 2020 (O'Neil et al. 2021).

2.3.6.3 Synthesis

At the time of listing, *D. cylindrus* was determined to be threatened. Factors that contributed to this determination included its uncommon to rare occurrence that made it more vulnerable to stochastic events and depensatory processes, its low recruitment and ability to recover from mortality events, and its susceptibility to threats that are predicted to increase in the future. It was not considered as endangered at the time of listing because there was little information on population decline, because it showed some evidence of resistance to bleaching in some portions of its range in some circumstances, and because exposure to threats was moderated by its inhabitation of multiple habitats that would experience highly variable thermal regimes at local and regional scales.

The range and distribution of *D. cylindrus* at the time of listing was characterized as uncommon to rare occurrence throughout most of the greater Caribbean in most reef environments between 1 to 25 m depth. Since the listing, the species has experienced a contraction in its range due to loss of almost all wild colonies in Florida from SCTLD. About 543 colonies of 123 Florida genotypes remain in captivity, and advances in understanding of reproduction, like time of spawning and flexibility in reproductive mode, as well as advances in land-based spawning techniques, hold some promise for sexual propagation that may make eventual reintroduction possible.

The population trend at the time of listing was unknown due to low abundance and infrequent encounter rate in monitoring programs. Since the listing, there have been new studies in Florida and Colombia that have repeatedly surveyed the same *D. cylindrus* colonies and found that the population trend is decreasing. In addition, the emergence of SCTLD since the listing has greatly impacted *D. cylindrus*. The species is highly susceptible to SCTLD and is often one of the first species to become infected. This is a change from the determination at the time of listing that *D. cylindrus* had some susceptibility to disease based on available prevalence data but an absence of progression and mortality rates. Surveys for SCTLD indicate that *D. cylindrus* experiences high disease prevalence and colony mortality and that colonies in locations affected by SCTLD, such as Florida, the US Virgin Islands, and the mainland coast of Mexico, have disappeared or become increasingly rare. Local extirpation has occurred both at specific sites in Mexico and the US Virgin Islands as well as regionally in Florida at a larger spatial scale.

At the time of listing, *D. cylindrus* was identified as having some susceptibility to ocean warming due to the mixed bleaching response observed. A new study on bleaching of *D. cylindrus* in Florida indicates high susceptibility to bleaching in 2014 but some resilience to a subsequent bleaching event in 2015 at some sites due to a change in the abundance of bleaching-resistant zooxanthellae. Furthermore, one study estimated the recovery time between bleaching events, in the absence of disease, to be 11 years. This is longer than the expected time between bleaching events that are predicted to occur annually by 2040-2043 (van Hooidonk et al. 2015).

The information presented in this status review indicates that *D. cylindrus* is at higher risk of extinction than it was at the time of listing. At the time of listing, *D. cylindrus* was determined to be at risk of extinction in the foreseeable future but not more imminently because there was little evidence of declining populations, it appeared to be resistant to temperature-induced bleaching in some locations under certain circumstances, and it was distributed across multiple habitat types and depths that would experience variability in temperature stress across geographic and temporal spatial scales. However, new information presented in this 5-year review indicates that there have been severe declines in the abundance and distribution of *D. cylindrus* in the northern portions of its range and that *D. cylindrus* is highly susceptible to SCTLD, which has emerged as a devastating new disease since the time of listing. Though SCTLD is not yet present in the southern Caribbean, the disease spread between 2014 and 2021 from Florida throughout the northern Caribbean including the Mesoamerican Reef System, the Bahamas, the greater Antilles, and as far south as St. Lucia in the lesser Antilles. In locations where SCTLD has been observed, *D. cylindrus* has experienced high prevalence, fast disease progression within infected colonies, and high mortality rates from the disease. The range of *D. cylindrus* has diminished with the loss of almost all wild colonies in Florida, and though the occurrence of *D. cylindrus* has historically been uncommon to rare, the species has become even more rare as a result of SCTLD, disappearing from sites in Mexico and the US Virgin Islands. Furthermore, no observed sexual recruitment has been reported in the wild, and reductions in population size and local extinctions will further inhibit the species' ability to persist and replenish diminished populations through asexual and sexual reproduction. Therefore, *D. cylindrus* is currently at risk of extinction in the wild and should be considered for up-listing to endangered.

2.3.7 MYCETOPHYLLIA FEROX

2.3.7.1 Biology and Habitat

2.3.7.1.1 New information on the species' biology and life history:

There has been no new information on the biology or life history of *M. ferox*.

2.3.7.1.2 Abundance, population trends (e.g. increasing, decreasing, stable), demographic features (e.g., age structure, sex ratio, family size, birth rate, age at mortality, mortality rate, etc.), or demographic trends:

Mycetophyllia ferox is an uncommon to rare species that has a low encounter rate in monitoring studies. Therefore, information related to species abundance, distribution, and trends is limited. There has been no published information on the abundance or population trends of *M. ferox* since the listing, but there are some unpublished data from benthic monitoring programs. Unpublished data from permanent monitoring transects in Florida show a decline in *M. ferox* percent cover, live tissue area, and density between 2014 and 2019 (Appendix 2, Figures 125-127). These patterns were similar in both the Dry Tortugas and the Florida Keys (no colonies were observed in the southeast Florida transects). Unpublished data from stratified random surveys (different sites surveyed each year) indicate that the percentage of sites in the US Virgin Islands and Puerto Rico with *M. ferox* present ranged from 0 to 2.5% and declined between 2014 and 2019 (Appendix 2, Figure 131). The percentage of sites with *M. ferox* present in Florida was variable with no clear trends (Appendix 2, Figure 131). Mean maximum colony diameter remained stable or increased in all locations over this same time period, and mean partial colony mortality was generally less than 20% (Appendix 2, Figure 132).

2.3.7.1.3 Genetics, genetic variation, or trends in genetic variation (e.g., loss of genetic variation, genetic drift, inbreeding, etc.):

There is no new information on genetics or genetic variation of *M. ferox*.

2.3.7.1.4 Spatial distribution, trends in spatial distribution (e.g. increasingly fragmented, increased numbers of corridors, etc.), or historic range (e.g. corrections to the historical range, change in distribution of the species' within its historic range, etc.):

There is no new information on spatial distribution of *M. ferox*.

2.3.7.2 Five-Factor Analysis (threats, conservation measures, and regulatory mechanisms)

2.3.7.2.1 Present or threatened destruction, modification or curtailment of its habitat or range:

Loss of recruitment habitat continues to be a threat to Caribbean corals, including *M. ferox*. The presence of algae can inhibit settlement of coral larvae, and in many locations in the Caribbean, there has been a shift from coral dominated to algal dominated reefs partially attributed to the loss of herbivores, including the Caribbean-wide die-off of the long spined sea urchin *D. antillarum* and the trophic effects of over-fishing. There is no new information about the magnitude of this threat to *M. ferox*.

2.3.7.2.2 Overutilization for commercial, recreational, scientific, or educational purposes:

Although *M. ferox* is susceptible to collection and trade, it is a low threat that did not contribute to its status. No new information indicates a change in the magnitude of this threat.

2.3.7.2.3 Disease or predation:

Disease

Since the listing, SCTLD has emerged as a new disease that impacts at least 24 Caribbean coral species, including five of the seven ESA-listed species (Florida Coral Disease Response Research & Epidemiology Team 2018). It was first observed in Miami, Florida in 2014 and then spread throughout the Florida reef tract over the next several years (Neely 2018; Precht et al. 2016). It has continued to spread throughout much of the Caribbean and has been observed along the Mesoamerican Reef, Bahamas, Greater Antilles, and as far south as St. Lucia in the Lesser Antilles (see https://www.agrra.org/coral-disease-outbreak/ for a map of confirmed sightings of SCTLD in the greater

Caribbean). The disease is unprecedented in temporal and geographic scope as well as the number of susceptible species, prevalence, and rates of mortality (Neely 2018; Precht et al. 2016). In almost all affected species, tissue loss occurs rapidly and leads to full colony mortality. The disease appears to be both water-born and transmissible through direct contact (Neely 2018). Unlike other coral diseases, it does not appear to be seasonal or subside with cooling water temperature. *Mycetophyllia ferox* is presumed to be susceptible to SCTLD, but there is not enough information to determine if it is one of the first species to succumb to the disease due to low population abundance and encounter frequency (Florida Coral Disease Response Research & Epidemiology Team 2018).

Predation

Mycetophyllia ferox has low susceptibility to predation, and there is no new information related to this threat.

2.3.7.2.4 Inadequacy of existing regulatory mechanisms:

The threats related to global climate change, including bleaching from ocean warming, ocean acidification, and increased disease (Maynard et al. 2015), pose the greatest potential extinction risk to corals and in the last review were evaluated with sufficient certainty out to the year 2100. We relied on information in the Intergovernmental Panel on Climate Change (IPCC) Fifth Assessment Report (AR5), Climate Change 2013: The Physical Science Basis (IPCC 2013), commonly referred to as the Working Group I Report (WGI). This report presented four Representative Concentration Pathways (RCPs) to simulate future climate change, and we evaluated extinction risk using RCP8.5 which represented the high emissions pathway we were currently on.

The IPCC is now in its sixth assessment cycle (AR6) and has released the WGI report Climate Change 2021: The Physical Science Basis (IPCC 2021) that addresses the most updated physical understanding of the climate system and climate change. The latest report indicates that greenhouse gases have continued to increase in the atmosphere since the 2011 measurements reported in AR5. Strong warming has been observed since 2012, and 2016–2020 was the hottest five-year period recorded since at least 1850. Global surface temperature was 1.09°C higher in 2011–2020 than in 1850–1900. On the current emissions trajectory (RCP8.5), the onset of annual severe coral bleaching in the Caribbean is predicted to occur in 2040-2043 with some regional variation (van Hooidonk et al. 2015); under RCP4.5, which represents lower emissions mid-century than will occur if pledges made following the 2015 Paris Climate Change Conference (COP21) become reality, annual coral bleaching is predicted to occur 11 years later, thus doing little to give corals more time to adapt and acclimate (van Hooidonk et al. 2016). Therefore, existing regulatory mechanisms have continued to be inadequate to protect against climate change and the threat it poses to corals due to ocean warming, ocean acidification, and related increases in disease.

AR6 considers 5 greenhouse gas scenarios: very low (SSP1-1.9), low (SSP1-2.6), intermediate (SSP2-4.5), high (SSP3-7.0), and very high (SSP5-8.5). The report indicates that global surface temperature will continue to increase until at least 2050 under all five emission scenarios considered in the report. Crossing the 2°C global warming level in the period 2041–2060 is "very likely" to occur under the very high emissions scenario (SSP5-8.5), "likely" to occur under the high emissions scenario (SSP3-7.0), and "more likely than not" to occur in the intermediate emissions scenario (SSP2-4.5). In the nearer term (2021-2040), the 1.5°C global warming level is "very likely" to be exceeded under the very high GHG emissions scenario (SSP5-8.5), "likely*"* to be exceeded under the intermediate and high emissions scenarios (SSP2-4.5 and SSP3-7.0), "more likely than not*"* to be exceeded under the low emissions scenario (SSP1-2.6) and "more likely than not*"* to be reached under the very low emissions scenario (SSP1-1.9). With additional global warming, there is high confidence that the frequency of marine heatwaves will continue to increase, particularly in the tropical ocean. There is "likely" to be a global increase in marine heatwaves of 2–9 times in 2081–2100 compared to 1995–2014 under the low emissions scenario (SP1-2.6) and 3–15 times under the very high emissions scenario (SSP5-8.5). Thus, projected warming is expected to increase in the future.

2.3.7.2.5 Other natural or manmade factors affecting its continued existence:

Ocean Warming

Mycetophyllia ferox is susceptible to ocean warming, but there is no new information related to this threat.

Acidification

Mycetophyllia ferox is susceptible to ocean acidification, but there is no new information related to this threat.

Sedimentation

Mycetophyllia ferox is susceptible to sedimentation, but there is no new information related to this threat.

Nutrients

Mycetophyllia ferox is susceptible to nutrients, but there is no new information related to this threat.

2.3.7.3 Synthesis

At the time of listing, *M. ferox* was determined to be threatened (in danger of extinction within the foreseeable future). Factors that contributed to the listing status included its uncommon to rare occurrence that made it more vulnerable to stochastic events and depensatory processes, its low recruitment and ability to recover from mortality events, its decline in Florida and likely decline in other locations, and its susceptibility to threats that are predicted to increase in the future. It was not considered as endangered (currently in danger of extinction) at the time of listing because exposure to threats was moderated by its inhabitation of multiple habitats across a wide depth range, including both shallow and mesophotic depths, that would experience highly variable thermal regimes at local and regional scales, and because population abundance was thought to be at least hundreds of thousands of colonies based on population estimates from Florida.

Since the listing, unpublished monitoring data indicate that the population continues to decline in surveyed locations. In Florida, there was a decline in percent cover, live tissue area, and density in permanent monitoring stations. Surveys of stratified random sites have shown a decline in the number of sites where *M. ferox* is present in Puerto Rico and the US Virgin Islands; the percentage of sites with *M. ferox* present in Florida was much more variable between years with no clear trends. This new information indicates that *M. ferox* populations continue to decline in at least some portions of its range.

At the time of listing, *M. ferox* was described as highly susceptible to disease. Since the listing, SCTLD has emerged as a new disease with devastating effects on many coral species. Whole colony mortality is common with SCTLD, and the disease appears to be moving across the Caribbean, affecting more and more locations, with no signs of seasonality or abatement. Although there is no species-specific information on prevalence of SCTLD for *M. ferox* due to its low population abundance and infrequent encounter rate, *M. ferox* is presumed to be susceptible to the disease. Thus, we conclude that the vulnerability of *M. ferox* to disease has increased since the time of listing.

In the listing determination, *M. ferox* was described as susceptible to ocean warming, ocean acidification, the trophic effects of fishing, nutrients, and sedimentation. There has been no new species-specific information on these threats since the listing.

In summary, populations of *M. ferox* appear to be continuing to decrease in some portions of its range. Information is very limited due to its low encounter rate and population size, but it still appears to inhabit its historical range. The susceptibility of *M. ferox* to threats identified at the time of listing has not changed, though the emergence of SCTLD has increased the vulnerability of *M. ferox* to disease. Based on all these factors, *M. ferox* continues to be at risk of extinction in the foreseeable future but does not appear to be currently at risk of extinction. Thus, no change in status is recommended at this time.

3.0 RESULTS

3.1 Recommended Classification

_____**Downlist to Threatened**
__X___**Uplist to Endangered** (*D. cylindrus*)
_____**Delist**
_____*Extinction*
_____*Recovery*
_____*Original data for classification in error*
___X__**No change is needed** (*A. cervicornis, A. palmata, O. annularis, O. franksi, O. faveolata, M. ferox*)

3.2 New Recovery Priority Number

No change for *A. cervicornis, A. palmata, O. annularis, O. franksi, O. faveolata,* and *M. ferox*

Change for *D. cylindrus* from 3C to 1C if up-listed to Endangered

Brief Rationale:

Demographic Risk: High if *D. cylindrus* is ultimately listed as Endangered. It is at or below depensation, has fragmented distribution, is a naturally rare species with a decreasing trend, and is likely functionally extinct in the northern portion of its range (Florida).

Major Threats Understood: High - Multiple threats include climate change, land-based sources of pollution, trophic effects of fishing, diseases, and depensatory effects. Disease is the most immediate major threat. Bleaching from warming water temperatures resulting from climate change is also a major threat that will continue to increase until substantial reductions in emissions of greenhouse gases occur.

U.S. Jurisdiction Exists: High - The range of *D. cylindrus* includes Florida and the greater Caribbean. The US has the authority and ability to address all of the local threats within its jurisdiction, and though climate change is a global problem, the US is a major emitter and can be influential in encouraging reductions in emissions by other nations. The US leads the development of response efforts to SCTLD, the greatest immediate threat to the species, and participates in regional work groups to share experience and effective strategies. The US also leads efforts for genetic banking and propagation of *D. cylindrus* which are tools to aid in restoration efforts.

Action will be Effective: High - While actions to abate climate change are difficult, they will be extremely effective. Actions to abate other threats, such as watershed management and reduction of overharvest of herbivores will also be effective. Novel recovery actions such as treatment of colonies infected with SCTLD and propagation of resilient genotypes are proving to be effective too.

Conflict: Yes –The species is in conflict with construction, development, or other forms of economic activity.

3.3 Listing and Reclassification Priority Number

Reclassification (from Threatened to Endangered) Priority Number:_1___
Reclassification (from Endangered to Threatened) Priority Number:____
Delisting (Removal from list regardless of current classification) Priority Number:__

Brief Rationale: The magnitude of the threats of climate change and disease are high, and the immediacy of the threat of disease is imminent.

4.0 RECOMMENDATONS FOR FUTURE ACTIONS

One recommendation is to make an effort to collect long-term demographic monitoring data for species in US jurisdiction. Demographic monitoring of *A. palmata* and *D. cylindrus* in the US Virgin Islands and Puerto Rico, or in other jurisdictions outside the US, would be helpful for future status reviews. Additionally, demographic monitoring of the three *Orbicella* spp. in all three US jurisdictions and/or from other locations in the wider Caribbean would provide insight into how the species are faring.

Another data need is to assess whether the distribution of the species within their ranges are changing. From available benthic monitoring data, we can sometimes see trends in percent cover, but as populations continue to decline and the species become less common, more targeted monitoring of the species will likely be needed in addition to general benthic monitoring. One recommendation is to periodically revisit sites where the species are known to occur to help assess whether they are disappearing from those sites.

There was little available information to evaluate the population status of *M. ferox* in this status review. Its low encounter rate, non-reef-building status, and the difficulty distinguishing it from conspecifics lead to less focus on the species in research and monitoring programs compared to the other ESA-listed coral species. More effort to collect abundance, distribution, and trend information for *M. ferox* is needed.

Dendrogyra cylindrus appears to be the most vulnerable to extinction of all the species examined in this review. Efforts to collect and preserve genetic material, such as sperm for cryopreservation and fragments for conservation, would be prudent. The species is already rare and is in serious danger from the threat of SCTLD as the disease continues to spread across the Caribbean. Preservation of genetic material would enable propagation and potential restoration in the future.

Another recommendation is to collect monitoring data from outside US jurisdictions. Some of the most informative trend data relied upon in this review was unpublished monitoring data from the US. Because publication of data often lags data collection by a few years, peer-reviewed literature is often less current than unpublished monitoring data. Therefore, more effort to locate and obtain monitoring data from the wider Caribbean would be beneficial.

Finally, only two of the species covered in this 5-year review have a recovery plan, and of the ten recovery criteria identified in the plan, three are interim. While the interim criteria and lack of a recovery plan for the other five species did not hinder this review or recovery efforts, another recommendation would be to develop final recovery criteria for *A. cervicornis* and *A. palmata*, and to develop a recovery plan for the other five species. Because the threats to all seven species are similar, the recommendation is to incorporate all seven species into one recovery plan and develop final recovery criteria for all the threats.

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NATIONAL MARINE FISHERIES SERVICE
5-YEAR REVIEW

Acropora cervicornis, Acropora palmata, Orbicella annularis, Orbicella faveolata, Orbicella franksi, Dendrogyra cylindrus, Mycetophyllia ferox

Current Classification: Threatened

Recommendation resulting from the 5-Year Review

☐ Downlist to Threatened
☒ Uplist to Endangered (*D. cylindrus*)
☐ Delist
☒ No change is needed (*A. cervicornis, A. palmata, O. annularis, O. franksi, O. faveolata, M. ferox*)

Review Conducted By (Name and Office):

Alison Moulding, Southeast Regional Office
Mark Ladd, Southeast Fisheries Science Center

REGIONAL OFFICE APPROVAL:

Lead Regional Administrator, NOAA Fisheries

Approve STRELCHECK.ANDREW.JAMES.1365863152 Digitally signed by STRELCHECK.ANDREW.JAMES.1365863152 Date: 2022.07.28 11:12:15 -04'00' Date: 7/28/22

Cooperating Regional Administrator, NOAA Fisheries

☐ Concur ☐ Do Not Concur ☒ N/A

Signature______________________________ Date: _______

HEADQUARTERS APPROVAL:

Assistant Administrator, NOAA Fisheries

☒ Concur ☐ Do Not Concur

Signature RAUCH.SAMUEL.D.III.1365850948 Digitally signed by RAUCH.SAMUEL.D.III.1365850948 Date: 2022.08.05 15:38:48 -04'00' Date: _______