Indo-Pacific Reef-building Corals:

General Status Assessment

The coral reef benthic community at Swains Island in American Samoa (NOAA Coral Reef Conservation Program).

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Executive Summary

This Status Assessment provides general information common to most or all Indo-Pacific reef-building coral species, including biology, habitat, trends, and threats. It is intended to be used in conjunction with species-specific information in other documents to support management efforts under the Endangered Species Act (ESA) for Indo-Pacific reef-building coral species, including status reviews, 5-year reviews, and recovery plans.

Reef-building coral species collectively produce coral reefs over time in high-growth conditions, typically in tropical and sub-tropical waters less than 30-40 meters (98-131 feet) deep. Some reef-building corals also occur in non-reef and mesophotic (>30-40 m) habitats, i.e., although reef-building, they are not reef-dependent. Of the world's 831 currently recognized species of reef-building corals, 758 species occur in the Indian and Pacific Oceans, otherwise known as the Indo-Pacific area. Biodiversity of Indo-Pacific reef-building corals is highest in the "Coral Triangle" area of eastern Indonesia and the southern Philippines (>600 spp.), and lowest in the peripheral areas such as the eastern Pacific and southern Australia (<50 spp.).

Indo-Pacific reef-building coral biology includes several general characteristics that provide both limitations and adaptability, and thus provide important context for species-specific management efforts: They are modular, colonial, and sessile organisms; there is a high degree of taxonomic and species identification uncertainty; coral-algae-microbe symbioses are a fundamental aspect of all colonies; the calcification process builds coral skeletons that have high plasticity in response to environmental variables; reproductive strategies are diverse and hybridization is common; and very large ranges are made possible by long-distance genetic connectivity. The habitat characteristics of Indo-Pacific reef-building corals also provide important context, including their habitat requirements in terms of substrate and water quality, the diversity of habitat types that meet these requirements, the spatial and temporal variability in their habitats, and the numerous types of spatial and temporal refuges from various threats.

Over the past few decades, there have been increases in the frequency, severity, and magnitude of anthropogenic disturbances to Indo-Pacific reef-building corals, two consequences of which are reduced time available for recovery of corals, and reduced coral cover. Indo-Pacific reef-building corals are inherently resilient, and overall resilience remains high. However, anthropogenic disturbance, recovery time, coral cover, and overall resilience are all projected to worsen in the 21st century (Table 1).

Table 1. Observed and projected trends in anthropogenic disturbance, recovery time, coral cover, and overall resilience of Indo-Pacific reef-building corals on shallow reefs (<30-40 m).

Trend	Observed*	Projected*
Anthropogenic Disturbance	↑	↑
Recovery Time	↓	↓
Coral Cover	↓	↓
Overall Resilience	O	↓

*Observed = from mid-20th century to present. Projected = from present to 2100. ↑ = a negative upward trend. ↓ = a negative downward trend. O = available information does not indicate any trend.

The most important threat to the continued existence of Indo-Pacific reef-building corals is ocean warming and subsequent warming-induced coral bleaching. Ocean warming is caused by global climate change, which refers to increased concentrations of greenhouse gases (GHGs, primarily carbon dioxide, CO_2) in the atmosphere from anthropogenic emissions, and subsequent warming of the earth and other impacts since the beginning of the industrial era in the mid-19th

century. According to the International Panel on Climate Change (IPCC), the global mean surface temperature has increased by nearly 1° C since 1850, and is currently increasing at 0.2° C per decade due to past and ongoing GHG emissions. The IPCC uses Representative Concentration Pathways (RCPs) to project potential trajectories of future climate change between the present and the year 2100. In this report, we consider the time period from the present to 2100 to be the "foreseeable future", and we assume that GHG emissions will continue to increase at their current rate over most of that time period as projected by the IPCC's high emissions pathway, RCP8.5.

There are numerous other threats to Indo-Pacific reef-building corals in addition to ocean warming. Ocean acidification poses a major threat by reducing coral calcification and reef cementation, resulting in lower skeletal growth and higher bioerosion. Sea-level rise threatens corals by potential reef submergence if reef accretion cannot keep up, and degradation of water quality by increased coastal erosion. Fishing threatens corals through direct habitat effects, as well as indirect trophic effects by reduction of herbivorous fish that control macroalgae that compete with corals for space. Land-based sources of pollution include sediment, nutrients, and contaminants that run off from coastal and watershed development, reducing water quality on coral reefs and directly affecting corals. Disease affects corals by causing adult mortality, reducing reproductive success and impairing colony growth, while predators reduce coral populations. Outbreaks of coral diseases and predators are exacerbated by the other threats. Live corals and coral skeletons collected from coral reefs for the marine aquarium and ornamental industry reduce coral populations and affect their habitat. Aside from these eight most important threats, other threats include changes in ocean circulation, changes in tropical storms, human-induced physical damage, invasive species, and reduced salinity from run-off. These threats may interact with one another, exacerbating the effects of each. Most threats have been observed to be worsening, and all are projected to worsen (Table 2). The inadequacy of existing regulatory mechanisms has exacerbated all threats, and is expected to continue to do so.

Table 2. Observed and projected trends of effects of threats on Indo-Pacific reef-building corals.

Threat	Observed*	Projected*
Effects of Ocean Warming	↑	↑
Effects of Ocean Acidification	↑	↑
Effects of Sea-level Rise	O	↑
Effects of Fishing	↑	↑
Effects of Land-based Sources of Pollution	↑	↑
Effects of Coral Disease	O	↑
Effects of Predation	O	↑
Effects of Collection and Trade	↑	↑
Effects of Other Global Threats	O	↑
Effects of Other Local Threats	↑	↑
Effects of Interactions of Threats	↑	↑

* Observed = from mid-20th century to present. Projected = from present to 2100. ↑ = a worsening trend. O = no trend discernable from available information.

1. Introduction

The purpose of this General Status Assessment is to provide contextual information necessary for the determination of the status of Indo-Pacific reef-building coral species under the Endangered Species Act (ESA). That is, this document provides general information common to most or all Indo-Pacific reef-building coral species, including biology, habitat, threats, and trends, that is intended to be used in conjunction with species-specific information in other documents to complete ESA status reviews. The General Status Assessment may also serve as a component of management efforts for Indo-Pacific reef-building corals that are already listed under the ESA, such as Recovery Plans and 5-year Reviews. It updates information provided in the 2011 Status Review Report (SRR) for 83 petitioned reef-building corals (Brainard et al. 2011) and the 2014 final coral listing rule (NMFS 2014), and will be periodically updated as new information becomes available.

This document follows Veron's geographic definition of the Indo-Pacific area, and list of Indo-Pacific reef-building coral species used in his Corals of the World website cited below, which builds upon his books and papers (Veron 2000a, Veron et al. 2015), and is accepted by most coral scientists. The Indo-Pacific includes all coral reefs in the Indian and Pacific Oceans (Fig. 1), which can be divided into 133 ecoregions based on reef-building coral and habitat characteristics (Veron 2015). Veron currently recognizes 831 species of reef-building corals in the world, including 758 Indo-Pacific species (http://www.coralsoftheworld.org, accessed January 2019), with the highest numbers in eastern Indonesia (>600 spp.) and the lowest in peripheral areas such as the eastern Pacific (<50 spp.)(Veron 2015).
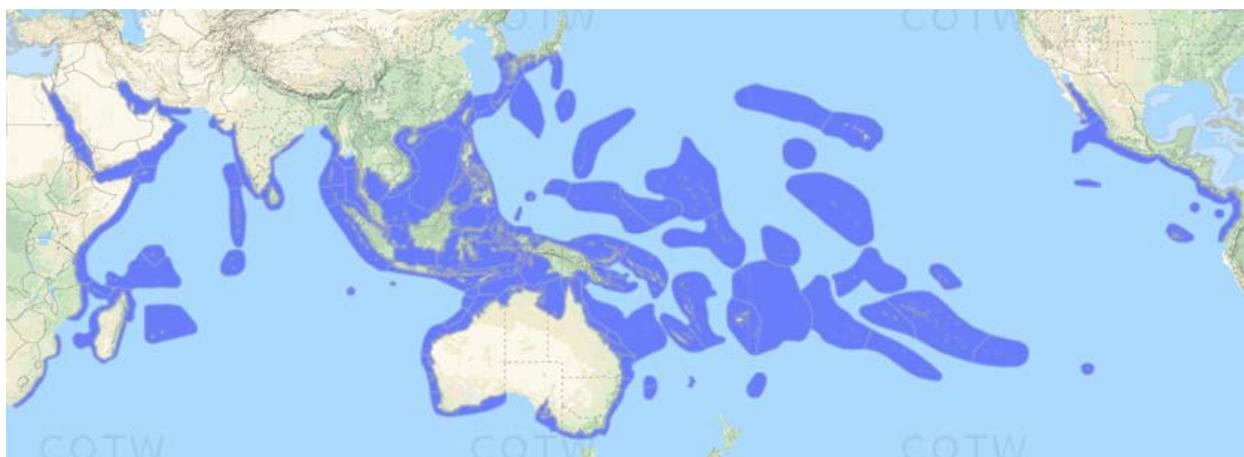
Figure 1. Ranges of Indo-Pacific Reef-building Corals. Map showing the collective ranges of 758 Indo-Pacific reef-building corals, based on Veron's 133 Indo-Pacific ecoregions (created on http://www.coralsoftheworld.org, January 2019).

This document includes chapters on Indo-Pacific reef-building coral biology and habitat, a threats evaluation, and trends in key characteristics. The biology and habitat chapter focuses on factors that complicate the determination of the status of species. The threats evaluation identifies the threats to the continued existence of Indo-Pacific reef-building corals, and descriptions of the observed and projected trends in each threat. The trends chapter reviews key characteristics of Indo-Pacific coral reefs (disturbance, recovery time, coral cover, and resilience), and descriptions of the observed and projected trends in each characteristic.

2. General Biology and Habitats of Indo-Pacific Reef-building Corals

Reef-building corals are defined by symbioses with unicellular photosynthetic algae living within their tissues (zooxanthellae), giving them the capacity to grow large skeletons and thrive in nutrient-poor tropical and subtropical seas. Since reef-building corals are defined by their symbiosis with zooxanthellae, they are sometimes referred to as "zooxanthellate" or "hermatypic" corals (Veron 2000a). Reef-building corals collectively produce shallow coral reefs over time, but these species also occur in non-reef and mesophotic habitats (shallow coral reefs, non-reef habitats, and mesophotic habitats are defined in the Habitat Diversity section below). That is, these species are reef-building, but they are not reef-dependent (Perry and Larcombe 2003).

Reef-building corals are marine invertebrates in the phylum Cnidaria that occur as polyps, usually forming colonies of many clonal polyps on a calcium carbonate skeleton. The phylum is named Cnidaria because organisms use cnidae (capsules containing stinging cells called nematocysts) for prey capture and self-defense. The Cnidaria include true stony corals (class Anthozoa, order Scleractinia, including both reef-building, zooxanthellate and non-reef-building, azooxanthellate species), the blue coral (class Anthozoa, order Helioporacea), and fire corals (class Hydrozoa, order Milleporina). Most reef-building corals form complex colonies made up of a tissue layer of polyps (a column with mouth and tentacles on the upper side) growing on top of a calcium carbonate skeleton, which the polyps produce through the process of calcification (Brainard et al. 2011). As of 2019, Veron estimates that 758 species of reef-building corals occur in the Indo-Pacific, over 90% of the world's total (Corals of the World, http://www.coralsoftheworld.org, January 2019).

2.1. Reef-building Coral Biology

Most Indo-Pacific reef-building corals have many biological features that complicate the determination of the status of any given species, including but not necessarily limited to the following: They are modular, colonial, and sessile; the definition of the individual is ambiguous; the taxonomy of many species is uncertain; field identification of species is difficult; each colony is a collection of coral-algae-microbe symbiotic relationships; they have high skeletal plasticity; they utilize a combination of sexual and asexual reproduction; hybridization may be common in many species; and they typically occur as many populations across very large ranges. These and other biological features of Indo-Pacific reef-building corals are described below.

2.1.1. Modular, Colonial, and Sessile Organisms

Most Indo-Pacific reef-building corals are both modular and colonial organisms: A larva will settle and develop into a single unit (the primary polyp), which then produces genetically-identical units (secondary polyps) of itself. Such colonial organisms are "modular", in that they consist of identical modules, in this case polyps. The primary and secondary polyps are connected seamlessly through both tissue and skeleton into a colony. Colony growth is achieved mainly through the addition of more polyps, and both the total number of polyps in a colony and colony growth, are indeterminate. Likewise, the colony structure is not strictly defined, providing plasticity in colony shape. The colony can continue to exist even if numerous polyps die, the colony is broken apart, or otherwise damaged. Colonies that are broken apart or that are clones can fuse back together. The biology of such modular, colonial species results in ambiguity with regard to many characteristics of an individual colony, complicating the collection of data needed to assess population status. For example, it can be difficult to delineate individual colonies in a population for several reasons (discussed further below), to determine when a

colony is dead because of partial mortality, and to determine the lifespan of a colony because both the number of polyps and colony growth are indeterminate (Hughes 1984, Hughes and Jackson 1980).

After larval settlement, the primary polyp and subsequent colony are anchored to the substrate and unable to move (sessile) in almost all species outside of the family Fungiidae, most of which occur as free-living solitary polyps. Corals build reefs because they secrete their own custom-made substrates which grow into skeletons, providing the primary building blocks for coral reef structure. Since space is a key resource for sessile organisms, competition for space is intense, especially for reef-building corals and other organisms that are dependent on photosynthesis, because they require space with adequate light. Successful sexual reproduction in sessile organisms (unless they are hermaphrodites) requires that colonies simultaneously spawn, and that colonies are close enough to one another so that gametes can be fertilized.

One of the most important aspects of sessile life history for consideration of extinction risk is that colonies cannot flee from unfavorable environmental conditions, and thus must have substantial capacity for acclimatization to the natural variability in environmental conditions at their location. Even the solitary species found in family Fungiidae have such limited motility that they are largely sessile from an ecological perspective. Likewise, since populations of a reef-building coral species are typically distributed throughout a large range with environmental conditions that vary by latitude, longitude, proximity to land, etc., the populations must have substantial capacity for adaptation to the natural variability in environmental conditions across their ranges. The capacity for both acclimatization and adaptation are key features for reef-building corals to survive changing environmental conditions (Brown and Cossins 2011, Coles and Brown 2003, van Oppen et al. 2015).

2.1.2.   Definition of the Individual

The colonial nature of most reef-building corals creates ambiguity with regard to definition of the individual, a key consideration under the ESA. Although the polyp could be considered as the smallest unit of the individual for reef-building corals, NMFS does not consider them individuals under the Endangered Species Act (ESA). Each polyp in a coral colony consists of a column of tissue with a mouth and tentacles on the upper side, growing in a cup-like skeletal structure (the corallite) made of calcium carbonate that the polyp produces through calcification. Polyps are the building blocks of the colony, and most colony growth occurs by increasing the number of polyps and supporting skeleton. Polyps carry out the biological functions of feeding, calcification, and reproduction. However, because polyps within a colony are modular units and connected to one another physiologically (i.e., connected via nerve net and gastrovascular cavity, and are the same sex), single polyps within a colony are not considered to be individuals for purposes of the ESA (NMFS 2014).

In this document, as in the 2014 ESA listings of 20 coral species (NMFS 2014), we use the concept of the "physiological colony" as the entity that can be considered an individual for reef-building colonial coral species that is useful for ESA-related evaluations. Colonies are founded by either sexually-produced larvae that settle and become the primary polyp of a colony, or asexually-produced fragments of pre-existing colonies that break off to form a new colony. Fragments from the same colony can fuse back together. Fragmentation in branching species may lead to a large number of asexually-produced, genetically identical colonies, commonly resulting in a population made up of more asexually-produced colonies than sexually-produced colonies (Hughes 1984). Sexually-produced colonies are important to the population because they increase its genetic diversity, whereas colonies originating from asexually-produced

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fragments do not contribute to the effective population (i.e., group of genetically unique individuals). Asexual reproduction, though it does not create new genetic individuals, is likely to be the more critical reproductive mode for some species, especially branching species because it allows them to grow, occupy space, and persist between relatively rare events of sexual reproduction. Sexually- and asexually-produced colonies are often morphologically very similar and can only be distinguished from one another through genetic analysis. Thus, we use the concept of the "physiological colony" as the entity that can be considered an individual. The physiological colony for reef-building colonial coral species is defined here as any colony of the species, whether sexually or asexually produced.

A physiological colony is generally autonomous from other colonies of the same species. However, colony morphology, partial colony mortality, and other colony growth characteristics (e.g., formation of stands or thickets) can complicate the identification of physiological colonies from one another in the field. For example, the overall colony morphology of many encrusting species (e.g., some *Montipora* species) is largely dictated by the underlying substrate. In those cases, colony shape may not distinguish colonies from one another, and boundaries between separate encrusting colonies that have grown together may be difficult or impossible to identify visually. Partial mortality of colonies, especially larger colonies, can also mask the boundaries between colonies, because the algae-encrusted coral skeleton of a partially dead colony may appear to delineate two or more colonies. In addition, many reef-building coral species occur in stands or thickets that may be tens of meters or more in diameter (e.g., some *Acropora* species), possibly consisting of multiple colonies or only one large colony. In each of these instances, the actual number of genetically-distinct individuals can only be determined through genetic analysis.

2.1.3. Taxonomic and Species Identification Uncertainty

A substantial complication in collecting data on Indo-Pacific reef-building corals is that both taxonomic and species identification is uncertain for most species. Taxonomic uncertainty refers to the incomplete knowledge of, or disagreement about, the taxonomic boundaries among species in the current classification system for Indo-Pacific reef-building corals. Taxonomic uncertainty of Indo-Pacific reef-building corals has many sources, including the large numbers of closely-related species (Veron 2000a), intra-specific skeletal variability (Forsman et al. 2009), the type specimen[1] having atypical morphology for the species (Fenner 2014), inconsistency between morphology-based and genetics-based species identification (Veron 2013), and the prevalence of hybridization (Forsman et al. 2010, Forsman et al. 2017). Many of these issues derive from the fact that corals are sessile species distributed across large ranges that encompass different types of environmental gradients, and most species have at least some phenotypic plasticity to respond to the specific conditions at a given site, thereby creating a large breadth of intra-specific morphological variation.

Species identification uncertainty refers to the level of difficulty in field identification of Indo-Pacific reef-building coral species. Species identification assumes that the current classification system on which field identification books and guides are based is correct. But as described above, the taxonomy of many species is unsettled, thus identification books and guides used in the field often contradict each other or are inconsistent. As with taxonomic uncertainty, these difficulties with species identification have several sources, including atypical morphology

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[1] Type Specimen: The particular specimen of an organism to which the scientific name of that organism is formally attached, typically stored in a museum and available for examination.

of a proportion of most species' colonies due to skeletal plasticity, poor quality of type specimens, lack of samples to verify photos of type specimens, inherent human subjectivity, and unreliable published information (Fenner 2014). While standardized species identification materials and training can greatly improve coral species identification results, it probably is not possible to consistently and reliably identify all colonies for most species due to the skeletal plasticity mentioned above. One of the first steps in evaluating a candidate for ESA listing is to determine if it meets the ESA definition of a species[2]; to do so for Indo-Pacific corals, we must address the taxonomic uncertainty and species identification difficulty for these organisms.

2.1.4.   Coral-Algae-Microbe Symbioses

Reef-building corals are able to grow and thrive in the characteristically nutrient-poor water environments of tropical and subtropical regions due to their ability to form mutually beneficial symbioses with unicellular photosynthetic algae living within the host coral's tissues (zooxanthellae) belonging to the dinoflagellate family *Symbiodiniaceae*. Zooxanthellae translocate fixed organic carbon and other nutrients to their host in return for inorganic waste metabolites from host respiration and protection from grazing. This exchange of nutrients allows both partners to flourish and helps the coral secrete calcium carbonate that forms the skeletal structure of the coral colony and contributes to the formation of the reef. Corals also host a wide range of non-photosynthetic microbes within their tissues and in their mucus, some of which, like zooxanthellae, are beneficial to the animal host. The coral animal host, its zooxanthellae, and its microbial community are sometimes referred to as a "coral holobiont" (Rowher et al. 2002, Bourne et al. 2009).

Reef-building corals have been found to harbor a wide variety of non-photosynthetic microbes, including fungi, bacteria, viruses, and others. Algae and cyanobacteria within the host coral's skeleton and tissues provides nutrition through nitrogen fixation, and a consortium of bacteria residing in the coral mucus layer acts as a first line of defense against pathogens. The highly diverse bacteria within the coral microbial community likely contribute to many important functions, such as protection of the host coral from bleaching (Mills et al. 2013), disease (Mao-Jones et al. 2011), ultra-violet radiation (Ravindran et al. 2013), and algal competition (Barrot et al. 2012). The complexity of a holobiont's internal symbiotic relationships between the host coral, zooxanthellae, and microbial community broadens its capacity for acclimatization and adaptation to changing environmental conditions (Putnam et al. 2017).

Reef-building corals act as plants during the day deriving nutrition from zooxanthellae photosynthesis (autotrophic feeding), and as animals during the night deriving nutrition from feeding on zooplankton (heterotrophic feeding). During daylight hours, they function as primary producers, and some species may obtain all of their daily caloric needs via photosynthetically-fixed carbon translocated from their zooxanthellae. However, neither the coral nor the zooxanthellae can actually grow on the energy-rich, nitrogen-poor "junk food" from photosynthesis – it may satisfy their caloric needs for maintenance but does not provide needed nutrients such as dissolved free amino acids. These nutrients must be obtained by predation, in which corals engage at night using nematocysts in their tentacles to capture zooplankton (Brainard et al. 2011).

The coral holobiont functions as a symbiosis of animal-algae-bacteria that is more complex than many other animals, and is also more sensitive to certain environmental changes

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[2] The ESA defines "species" as "includes any subspecies of fish or wildlife or plants, and any distinct population segment of any species or vertebrate fish or wildlife which interbreeds when mature."

than many other animals. For example, ocean warming can result in the bleaching of the tissues of reef-building coral colonies, whereby zooxanthellae are expelled in response to stress. For many reef-building coral species, an increase of only 1° C – 2° C above the normal local seasonal maximum ocean temperature can induce bleaching. Corals can withstand mild to moderate bleaching; however, severe, repeated, or prolonged bleaching can lead to colony death. Coral host interactions with multiple clades of zooxanthellae may provide the ability to adapt to different environmental conditions, but the capacities of the coral hosts to shuffle the most functional zooxanthellae types in response to changing environmental conditions is poorly understood and may be highly specific to the host coral species (Brainard et al. 2011). Ocean warming and warming-induced bleaching events are projected to become more frequent and severe, as described in the Ocean Warming section of the Threats Evaluation section below.

2.1.5.   Calcification and Skeletal Plasticity

The structure of coral reefs is provided primarily by the calcification and gradual accretion of reef-building coral skeletons, hence the term "reef-building." The process of calcification occurs within the tissues of reef-building corals, whereby calcium and carbonate ions derived from seawater are combined into calcium carbonate crystals. These are packed into bundles and stacked to form the coral's intricately designed skeleton which both supports and protects it. Because carbonate ions are rare in seawater, corals must convert the more plentiful bicarbonate ions into carbonate ions, and this process requires metabolic energy. Corals bring bicarbonate ions from seawater into internal extracellular compartments, where they physiologically maintain elevated pH that allows the conversion of bicarbonate to carbonate ions, which are then combined with calcium for precipitation as calcium carbonate crystals (Cohen and Holcomb 2009).

Calcium carbonate occurs in two different crystal forms, calcite and aragonite. Reef-building coral skeletons are predominantly composed of the aragonite form. The skeleton calcification process is enabled in the polyps by the manipulation of the chemistry of seawater within their tissues to produce aragonite crystals. The lower the level of aragonite in the external seawater (measured as aragonite saturation state, Ω_{arg}), the more energy the coral has to expend for skeletal calcification. As external seawater Ω_{arg} declines, coral skeletal calcification slows down and eventually stops. If Ω_{arg} declines too much, coral skeletons start to dissolve (Cohen and Holcomb 2009). Generally, Ω_{arg} of seawater should be 3.5 or greater to enable maximum calcification of reef-building corals (Brainard et al., 2011). However, Ω_{arg} of seawater is projected to drop below that level throughout the Indo-Pacific in response to ocean acidification, which results from global climate change, as described in detail in the Ocean Acidification section of the Threats Evaluation section below.

Each coral polyp builds its own skeleton (the corallite) out of aragonite crystals, and the corallites together make up a coral colony's skeleton. Once formed, the skeleton is external to the coral's tissue, thus the corallites provide a substrate for the polyps to sit upon. The shapes and sizes of both the corallites and the colony skeletons of the approximately 760 species of Indo-Pacific reef-building coral species are extremely variable. The shapes of the colony skeleton, or growth forms, can be categorized as massive, encrusting, branching, arborescent, columnar, and laminar. The shapes and sizes of corallites and colony skeletons are usually used together as the primary morphological characteristics used for identification of reef-building coral species. The growth rates of coral colony skeletons are highly dependent on taxa and environment, typically varying from an annual skeletal extension rate of about 1 cm for colonies

of some massive species to about 30 cm for colonies of some branching species (Corals of the World website, http://www.coralsoftheworld.org, February 2019).

The overall level of morphological plasticity varies substantially between species from low to very high. In addition, many Indo-Pacific reef-building coral species display considerable intraspecific morphological plasticity in skeletal structure within and between colonies, leading to a great deal of variability in growth forms within a single species (Buddemeier and Kinzie 1976, Todd 2008). As noted above, such plasticity is a source of much of the taxonomic uncertainty and species identification difficulties.

2.1.6. Reproduction, Hybridization, and Connectivity

Reef-building corals use a number of diverse reproductive strategies, and most species utilize both sexual and asexual propagation. Sexual reproduction in corals is primarily through gametogenesis, which occurs through development of eggs and sperm within the polyps. Some coral species have separate sexes, while others are hermaphroditic. Fertilization and larval development occur either internally within the polyps for brooders, or externally for broadcast spawners. Asexual reproduction in coral species most commonly involves fragmentation, where colony pieces or fragments are broken off of or dislodged from larger colonies and go on to reattach to substrate and establish new colonies. The budding of new polyps within a colony is also considered a form of asexual reproduction. In many species of branching corals, fragmentation is a common and sometimes dominant means of propagation. Coral larvae experience high mortality from predation or other factors prior to settlement and metamorphosis, as inferred from the large number of eggs and sperm spawned versus the much smaller number of recruits observed later. Coral larvae are relatively poor swimmers; thus, dispersal distances largely depend on the duration of the pelagic phase and the speed and direction of water currents transporting the larvae. Brooded larvae can settle shortly (hours) after release, but can also survive for periods of approximately 30 – 100 days in the water column. Spawned larvae have been documented to survive for periods of >200 days in the water column (Brainard et al. 2011).

Settlement of coral larvae occurs on hard substrates such as dead coral skeletons in response to appropriate cues, including chemical cues from crustose coralline algae or microbial films and acoustic cues from reef environments. Calcification of the initial corallite and growth of the primary polyp begins with the forming of the basal plate, from which buds develop into daughter corallites and polyps. Many physical and biological factors determine the success of reef-building coral recruitment, including substrate availability, chemical and acoustic cues, storm prevalence, ocean currents, grazing pressure, timing of reproduction, parent colony fecundity, brooding vs. broadcast spawning, larval behavior, and structure of established coral assemblages. Once larvae settle onto appropriate hard substrate, metabolic energy is diverted to colony growth and maintenance. Post-settlement benthic stages are highly vulnerable and poorly understood, due to their extremely small size and, in many species, slow growth rates, with the transition from primary polyp to a visible juvenile colony taking from three to 12 months. The transition from visible juvenile colony to reproductive adult colony may range from one to several (5–10) years (Brainard et al. 2011).

Many reef-building corals readily hybridize with one another, and numerous lineages appear to have undergone repeated cycles of divergence and convergence via hybridization, which has been termed "reticulate evolution" (Veron 2000b). Hybridization is thought to be one of the main reasons why such high diversity of reef-building coral species occurs on Indo-Pacific reefs (Vollmer and Palumbi 2002). The high potential for hybridization and introgression (gene flow from one species into the gene pool of another by the repeated backcrossing of an

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interspecific hybrid with one of its parent species) may convey adaptive capacity in some coral species, and likely is an important mechanism of diversification and potential adaptation to changing environments, which could be crucial to species' viability in an era of rapidly changing climate and ocean chemistry (Brainard et al. 2011). Hybridization is also likely one of the major sources of both taxonomic and field identification uncertainty in Indo-pacific reef-building corals, as it is often difficult to determine whether observed morphological variability is due to plasticity within a species, or hybridization of that species with another species (Forsman et al. 2017).

Genetic connectivity refers to the dispersal of coral larvae among spatially-distinct population patches within a larger metapopulation structure, and their successful settlement and reproduction (Edmunds et al. 2018). Some Indo-Pacific reef-building corals, such as *Pocillopora meandrina*, have very large ranges extending more than halfway around the world from the western Indian Ocean to the eastern Pacific Ocean. Such immense ranges are maintained by genetic connectivity at various spatial scales, which facilitates the recovery of populations following disturbances (Wood et al. 2014). For a given population, utilization of genetic connectivity with other populations together with self-recruitment confers resilience because the populations persist with a combination of recruits from either that population or one further away (Sale et al. 2010). Genetic connectivity can be maintained by populations on reefs that are highly connected by ocean currents. Those that have a relatively low risk of exposure to disturbances, such as crown-of-thorns outbreaks, are likely to provide replenishment to other reefs when depleted. On the Great Barrier Reef (GBR) of Australia, such "robust source reefs" make up only about 3% of the GBR, demonstrating how a small proportion of a species' range may impart resilience via connectivity (Hock et al. 2017). While there was some disagreement with these results (Bode et al. 2018, Mumby et al. 2018), a key underlying point of this connectivity research is that there is great heterogeneity in the habitats of coral reef species, with some habitat types, and therefore reef areas, having far greater potential than others to stimulate regional recovery. The importance of habitat heterogeneity to the future outlook of Indo-Pacific reef corals is discussed in more detail in the Habitat section below.

Many Indo-Pacific reef corals occur at mesophotic depths (>30-40 m), which are very extensive throughout the region and may provide important refugia from threats such as ocean warming (Bridge et al. 2012a, Kahng et al. 2014). Thus, genetic connectivity between shallow (<30-40 m) and deep (>30-40 m) reef coral populations may be important. A review of mesophotic habitat on Australia's GBR concluded that reef-building corals in mesophotic habitat are less likely to be affected by warming-induced bleaching events than their counterparts on nearby shallow reefs (Bridge et al. 2012b). Mesophotic habitat may also be important for recovery of corals on disturbed coral reefs by providing sources of propagules to recolonize shallow reefs following disturbances (Bridge and Guinotte 2013), although recent studies suggest these refugia effects are limited at best (Frade et al. 2018). A 37-year record from the eastern Pacific across the two most severe El Niño events on record (1982–83 and 1997–98) shows how an exceptionally thermally-sensitive reef-building fire coral, *Millepora intricata*, twice survived catastrophic bleaching in a deeper water refuge (>11 m depth). During both events, *M. intricata* was extirpated across its range in shallow water but showed recovery within several years, while two fire corals without deep-water populations were driven to regional extinction (Smith et al. 2014). Genetic connectivity between shallow and deep populations is high in *Seriatopora hystrix* on the GBR (van Oppen et al. 2011) and *M. intricata* in the eastern Pacific (Smith et al. 2014). However, a review of reef corals, even though mostly Atlantic species, found that genetic

connectivity between shallow and deep populations of reef corals was highly species-specific, and thus that high connectivity should not be assumed (Bongaerts et al. 2017).

2.2. Reef-building Coral Habitats

As defined in the Introduction above, the Indo-Pacific region encompasses the tropical and sub-tropical waters of the Indian and Pacific Oceans, including the eastern Pacific. This vast region includes over 50,000 islands and over 40,000 km of continental coastline, spanning approximately 180 degrees of longitude and 60 degrees of latitude, and including more than 90% of the total coral reefs of the world. In addition, the Indo-Pacific includes abundant non-reef habitat, as well as vast but scarcely known mesophotic areas that provide coral habitat. The amount of non-reef and mesophotic habitat that could currently be occupied by corals in the Indo-Pacific is unknown, but is likely greater than the area of shallow coral reefs in the Indo-Pacific (NMFS 2014).

In addition to the biological features described above, there are several features of the habitats of Indo-Pacific reef-building coral species that should be considered in the determination of the status of any given species including, but not necessarily limited to, specific substrate and water quality requirements for each life history stage; the ranges of many of these species which encompass reef and non-reef habitats and vary tremendously across latitude, longitude, depth, distance from land, and in other ways; and the physical variability which is found within the ranges of these species and thus produces spatial and temporal refuges from threats. These and other habitat features of Indo-Pacific reef-building corals are described below.

2.2.1. Habitat Requirements

Habitat requirements for the normal function of Indo-Pacific reef-building coral life history stages (reproduction, recruitment, growth, and maturation) include suitable substrate and water quality. For substrate, the appropriate type of substrate and low levels of sediment are required. For water quality, suitable seawater temperatures, aragonite saturation state, nutrients, water clarity, and salinity, together with low levels of turbidity and contaminants, are required. Suitable water motion is also required. These general habitat requirements for reef-building corals are described below.

Substrate. Consolidated hard substrate is required for the settlement and recruitment of larvae or asexual fragments of most species. Substrate provides the physical surface and space necessary for settlement of coral larvae, and a stable environment for metamorphosis of the larvae into the primary polyp, growth of juvenile and adult colonies, and re-attachment of fragments. Positive cues for coral larval settlement include the presence of crustose coralline algae (Tebben et al. 2015), biofilms (aggregates of microorganisms embedded within a self-produced matrix on a surface; Hadfield and Paul 2001), and cryptic habitat such as crevices and holes (Nozawa 2008). Negative cues for coral larval settlement include the presence of sediment (Babcock and Smith 2002, Ricardo et al. 2015) and algae. In addition to preempting space for coral larvae settlement, many fleshy macroalgae produce substances that may inhibit larval settlement, recruitment, and survival (Webster et al. 2015).

Sediment accumulation reduces the amount of available substrate for coral larvae settlement and fragment reattachment, and affects adult coral colonies by smothering and burial of coral polyps, shading, tissue necrosis, and population explosions of bacteria in coral mucus (Rogers, 1990; Erftemeijer et al. 2012). Sediments enter the reef environment through many processes that are natural or anthropogenic in origin, including erosion of coastline, resuspension of bottom sediments, terrestrial run-off, and nearshore dredging for coastal construction projects and navigation purposes (Erftemeijer et al. 2012). The depth of sediments over hard substrate

affects the duration that the substrate may be unavailable for settlement. The deeper the sediment, the longer it may take for waves and currents to remove the sediment from the settlement substrate. Sediment texture also affects the severity of impacts to corals and recruitment substrate. Fine grain sediments have greater negative effects to live coral tissue and to recruitment substrate (Erftemeijer et al. 2012). Accumulation of sediments is also a major cause of mortality in coral recruits (Fabricius et al. 2003). In some instances, under heavy sediment conditions, settled coral planulae may undergo reverse metamorphosis and die in the water column (Te 1992). Sediment texture also affects the severity of impacts to adult corals, and recruitment substrate. Fine grain sediments have greater negative effects to live coral tissue because they block more light, adhere more readily to coral tissue, and contain higher bacteria loads than coarse sediments (Erftemeijer et al. 2012). Sedimentation, therefore, impacts the health and survivorship by reducing available substrate for recruitment (larvae) and reattachment (fragments), smothering recently-settled recruits, reducing light availability for zooxanthellae (all life history stages), interfering with feeding (all life history stages), and inhibiting reproduction (adults).

       <u>Water Quality</u>. Suitable seawater temperatures are required for the successful completion of all life history stages. Although reef-building corals occur across a range of mean seawater temperatures (at least 18–32° C), most species tend not to thrive in areas with mean temperatures outside a fairly narrow range (typically 25–30° C). The primary observable coral response to warming seawater temperatures is bleaching of adult coral colonies, wherein corals expel their symbiotic zooxanthellae in response to stress. For many reef-building coral species, an episodic increase of only 1–2° C above the normal local seasonal maximum seawater temperature can induce bleaching. Corals can withstand mild to moderate bleaching, but severe, repeated, or prolonged bleaching can lead to colony death. Other impacts of warming seawater temperatures include impaired fertilization, impaired settlement success, reduced calcification, and other effects (Brainard et al. 2011). Spatial variability in seawater temperatures results from latitude, depth, mixing (e.g., wind, currents, tides, upwelling), shading (e.g. turbidity, cloud cover), and other factors. Temporal variability in suitable seawater temperatures results from tidal cycles, seasonality, storms, inter-decadal variability (e.g. El-Niño Southern Oscillation), and other factors (NMFS 2014).

       As described above in the Calcification and Skeletal Plasticity section above, suitable ranges of aragonite saturation state (Ω_{arg}) are necessary for skeletal growth. Reef-building corals produce skeletons made of the aragonite form of calcium carbonate, thus reductions in aragonite saturation state inhibit coral calcification, reducing skeletal growth rates of colonies. In addition, declining aragonite saturation state may weaken reef accretion and cementation, leading to increased reef erosion. Spatial variability in seawater pH and subsequent aragonite saturation state occurs from reef to global scales, driven by numerous physical and biological characteristics and processes, including seawater temperature, proximity to land-based runoff and seeps, proximity to sources of oceanic carbon dioxide (CO_2), salinity, nutrients, photosynthesis, and respiration. In cooler waters, CO_2 absorption is higher, driving pH and aragonite saturation state lower, thus relatively cool coral habitats are more susceptible to acidification, such as those at higher latitudes, in upwelling areas, and in deeper environments. Temporal variability over various time-scales results from numerous processes, including diurnal cycles of photosynthesis and respiration, seasonal variability in seawater temperatures, and decadal cycles in upwelling. Temporal variability in pH can be very high diurnally in highly fluctuating or semi-enclosed habitats such as reef flats and back-reef pools due to high

photosynthesis during the day (pH goes up) and high respiration during the night (pH goes down), with subsequent fluctuations in aragonite saturation state (NMFS 2014).

Suitable nutrient levels are necessary for the successful completion of all life history stages. Elevated nutrients affect corals through two main mechanisms: direct impacts on coral physiology, and indirect impacts through nutrient stimulation of other community components (e.g., macroalgae seaweeds, turf/filamentous algae, cyanobacteria, and filter feeders) that compete with corals for space on the reef. Nutrients can also stimulate plankton growth and thus increase turbidity. Dissolved inorganic nutrients (nitrates and phosphates) are needed for plant growth, so they stimulate the growth of both free-living algae and the zooxanthellae within coral tissues. The growth of free-living algae is also partly controlled by herbivores, so nutrients are more likely to cause algae increases when herbivore populations are low (Brainard et al. 2011). Dissolved inorganic nitrogen and phosphates both have a moderately strong effect of increasing photosynthesis in zooxanthellae, and nitrogen has a strong effect of increasing zooxanthellae density (Fabricius 2005). For example, high nitrogen levels have been shown to increase zooxathellae populations beyond the optimum sizes thus imposing an energetic cost on the coral (Wooldridge 2014). High nitrogen levels also may increase bleaching in high temperatures, because the increased nutrient levels lead to higher zooxanthellae density but lower energy transferred to the coral host, making the coral more susceptible to stressors such as elevated seawater temperatures. Dissolved inorganic nutrients inhibit fecundity, fertilization, embryo and larval development, and possibly larval settlement (Fabricius 2005).

Suitable water clarity is necessary for the successful completion of all life history stages. Indeed, water clarity is so important for corals that clarity is the best explanatory variable for a range of bioindicators of reef health on the GBR (Fabricius et al. 2012). Turbidity reduces water clarity, and is caused by the presence of particles of sediment, organic matter, or plankton in the water, which is often associated with elevated sedimentation or nutrients. Corals need light for their zooxanthellae to photosynthesize and provide the coral with food, thus low turbidity is needed for coral energy, growth and survival. Higher turbidity and subsequent lower water clarity sharply reduces photosynthesis in zooxanthellae and calcification, with moderate reductions in adult colony survival and calcification. Reduced water clarity also restricts the depth at which corals can live, making otherwise suitable deeper habitat uninhabitable. Suspended particulate matter reduces pre-settlement survival of coral larvae and shading alters coral larval settlement (Fabricius 2005).

Chemical contaminants must be at minimal levels to avoid affecting corals. The major groups of contaminants that have been studied with regard to their effects on corals include heavy metals (also called trace metals), pesticides, and hydrocarbons. Other organic pollutants, such as chemicals in personal care products, have also been studied. These pollutants have negative effects on coral reproduction, development, growth, photosynthesis, and survival (Brainard et al. 2011, SERO 2016). Contaminants may be delivered to coral reefs via either point or non-point sources. Specifically, they enter the marine environment through wastewater discharge, shipping, industrial activities, and agriculture and urban runoff.

Suitable water motion is necessary for the successful completion of all life history stages. Water motion occurs across spatial scales from local (<1 m) to regional (thousands of km) and is caused by waves, surge, tides, upwellings, and currents. Water motion influences the growth, mortality, and reproduction of corals, and many species are adapted to specific hydrodynamic conditions. For example, in Hawaii, *Pocillopra meandrina* is primarily found in environments with high water motion from waves and surge (Jokiel 1978). Water motion may provide

protection to corals by increasing their thermal tolerance to bleaching (Lenihan et al. 2008; Nakamura and Yamasaki 2005), facilitating diffusion of toxic metabolites, and increasing access to food (Brainard et al. 2011).

2.2.2. Habitat Diversity

Reef-building coral species are not restricted to coral reefs, but also occur in non-reef and mesophotic habitats in tropical and sub-tropical seas. Reef-building corals were defined in the introduction to this General Biology and Habitats section as corals with zooxanthellae, which give them the capacity for rapid skeletal growth, and is the basis for reef building. Coral reefs can be defined in different ways. Here, shallow coral reefs are defined as complex three-dimensional structures occurring from the surface to 30-40 meters of depth resulting from the skeletal growth of reef-building organisms including corals (Veron 2000a). Non-reef habitats are defined as areas where environmental conditions prevent reef formation by reef-building corals, but some reef-building coral species are present (Perry and Larcombe 2003). Mesophotic habitats are defined as areas deeper than 30-40 meters of depth where reef-building corals occur (Kahng et al. 2014), whether as reefs or not. While shallow coral reefs, non-reef habitats, and mesophotic habitats are not strictly delineated from one another, they each have particular characteristics, as described more below.

Shallow Coral Reefs. The three broad categories of shallow coral reefs are fringing reefs, barrier reefs, and atolls. Fringing reefs run along coastlines, barrier reefs are further offshore but still associated with land, and atolls are typically far from land. Fringing reefs and barrier reefs are usually linear, often following the shape of coastlines, while atolls are normally a ring of reef enclosing a lagoon. There are not sharp differences that clearly mark boundaries between reef types, or between reefs and non-reef areas. For example, fringing reefs gradually become barrier reefs with increasing distance from shore. Also, the shapes of barrier reefs and atolls are largely determined by the bathymetry of the substratum, producing many irregularly shaped reefs that are intermediary between the two types. Isolated reefs that do not fit any of these descriptions are referred to as platform reefs (Veron 2000a).

Despite the differences between the reef categories, most fringing reefs, barrier reefs, atolls, and platform reefs consist of a forereef, a reef crest, and a back-reef, which in turn are typically characterized by distinctive habitats. The forereef (or reef slope) is the seaward side of the coral reef between the reef crest and the deep ocean, and generally includes upper forereefs or reef slopes (approximately 5-10 m depth), mid-slopes that often occur as terraces or shelves (approximately 10-30 m depth), and lower reef slopes or walls (approximately 30-40 m depth) that form the transition to mesophotic habitats (greater than 30-40 m depth). The reef crest (approximately 0-5 m depth) forms the boundary between the forereef and back-reef, and generally includes a consolidated ridge or rim where the waves break, and a lower reef crest on the seaward side of the algal ridge often made of up of buttresses and surge channels (i.e., spur-and-groove structures). The back-reef lies between the reef crest and land (or middle of the lagoon, in the case of atolls). The back-reef generally includes reef flats (approximately 0 to 1-5 m depth) and lagoons (approximately 1-5 to over 30 m depth), interlaced with tide pools, channels, patch reefs, and other features. The characteristics of these habitat types vary greatly by reef categories, locations, latitudes, frequency of disturbance, etc., and there is also much habitat variability within each habitat type, together constituting the habitat heterogeneity of coral reefs, as described further below.

Fringing reefs occur adjacent to coastlines, and subsequently the habitats associated with their reef slopes and back-reefs may be quite different than on barrier reefs or atolls. The reef

slopes of many fringing reefs that are protected from strong wave action (e.g., on leeward sides of islands) consist of unconsolidated material sloping gently towards deeper water, while those of fringing reefs in more exposed areas (e.g. windward sides of islands) are usually more consolidated. On many fringing reefs, even on the reef slope, natural turbidity and sedimentation may be high due to proximity to land. Fringing reefs typically have narrow back-reefs consisting of a reef flat abutting the reef crest, and possibly tide pools, channels, or small lagoons between the reef flat and shore (Goreau 1959; Veron 2000a).

Barrier reefs typically form tens to hundreds of kilometers from coastlines. Their reef slopes are composed of consolidated limestone that may plunge steeply to deeper water, and natural turbidity and sedimentation are very low due to distance from land. Thus the characteristics of their reef slope habitats can be quite different than on fringing reefs. Barrier reefs are exposed to very strong wave action, and their reef crests can vary from high, consolidated algal ridges, to unconsolidated shingle ramparts, to low and wide indistinct crests. In addition, barrier reefs typically have immense back-reefs consisting of reef flats abutting the reef crest, and large lagoons that may vary from clear and sandy near the reef to turbid and muddy near land, and include various features such as patch reefs and islands (Maxwell 1968).

Atolls occur in oceanic waters far from land, and may be hundreds of kilometers across. Their reef slopes often form vertical walls dropping into abyssal waters, and their back-reefs consist of large, clear lagoons (Veron 2000a).

Environmental conditions vary greatly among the habitat types found on the reef slopes, reef crests, and back-reefs of the world's coral reefs. In addition, much variability also occurs within each habitat type. For example, Maxwell (1968) describes six geomorphological types of reef crests, and how the different environmental conditions provide "coral zones" unique to each type of reef crest. The physical diversity of coral reef habitat is illustrated by Kuchler (1986), who notes that the scientific literature on the GBR alone used over 20 terms for the reef slope or its habitats, over 50 terms for the reef crest or its habitats, and over 100 terms for the reef flat and lagoon and their habitats.

In conclusion, five main points are important regarding coral habitat on shallow coral reefs (as opposed to non-reef and mesophotic habitats): (1) Regardless of reef category, reefs generally consist of forereefs (reef slopes), reef crests, and back-reefs, each of which have distinct habitats, but those habitats can be highly variable between reef types and locations; (2) spatial variability in coral habitat conditions is very high between habitat types, as well as within the habitat types described above (i.e., deep reef slopes, walls, mid-slopes, upper reef slopes, lower reef crests, algal ridges, reef flats, and lagoons), producing highly variable environmental conditions across both large and small spatial scales at any given point in time; (3) temporal variability in coral habitat conditions is also very high, both cyclically (e.g., from tidal, seasonal, annual, and decadal cycles) and episodically (e.g., storms, temperature anomalies, etc.); (4) together this spatial and temporal variability in environmental conditions across multiple scales produces the very high habitat heterogeneity of coral reefs; and (5) while most coral species are more common in certain reef habitat types, they are typically found in many different habitat types.

Non-reef and Mesophotic Habitats. As described in Habitat Requirements above, reef-building corals have specific habitat requirements, including hard substrate, narrow range of seawater temperatures, adequate light, etc. These habitat requirements most commonly occur on the shallow coral reefs described above, but also occur in non-reef and mesophotic areas. Non-reef habitats are defined as areas where environmental conditions prevent reef formation by reef-

building corals, but some reef-building coral species are present (Perry and Larcombe 2003). Mesophotic habitats are defined as areas deeper than 30-40 meters of depth where reef-building corals occur (Kahng et al. 2014), whether as reefs or not. The widely used term "mesophotic reefs" is subsumed in this definition of mesophotic habitats. Shallow coral reefs, non-reef areas, and mesophotic areas are not necessarily sharply delineated from one another, thus one may gradually blend into another. The total area of non-reef and mesophotic habitats is likely far greater than the total area of shallow coral reef habitats in the Indo-Pacific (NMFS 2014).

Non-reef habitats include some marginal habitats (Perry and Larcombe 2003), as well as newly available natural habitats such as hard substrates created by lava flows (Grigg and Maragos 1974), tsunamis (scoured bedrock or transported boulders, Goto et al. 2010), or other episodic processes. Marginal habitats are much more common than newly-available natural habitats. Marginal habitats are very diverse, as they occur where seawater temperatures or light levels are sub-optimal (i.e., inadequate for high skeletal growth but still allowing reef-building corals to survive), and thus include environments that are turbid (Browne et al. 2012, Blakeway et al. 2013), very warm (Riegl et al. 2011, Riegl and Purkis 2012) or cold because of high latitude (Lybolt et al. 2011, Dalton and Roff 2013) or upwelling (Manzello et al. 2008, Alvarado et al. 2011), and other environments (Perry and Larcombe 2003, Couce et al. 2012). Such habitat is not necessarily indicative of low-diversity coral assemblages, as shown by turbid sites, which have been documented to support over 160 species of reef-building corals (Perry and Larcombe 2003), and fresh lava flows, which have been documented to support fully recovered coral communities only 20 years after the flow (Grigg and Maragos 1974). Marginal habitats expand the diversity of environmental conditions that can support some reef-building corals and therefore may provide refugia from some threats affecting shallow coral reef habitat, as described in the Refugia sub-section below.

Over the last 15 years, research on mesophotic habitats has demonstrated that many reef-building corals have greater depth distributions than previously reported. These studies demonstrate that some species in shallow coral reef habitats readily extend to mesophotic depths if water clarity and temperatures remain favorable (Kahng et al. 2014). For example, investigations in American Samoa (Bare et al. 2010), the Hawaiian Archipelago (Kahng et al. 2010, Rooney et al. 2010), and the Mariana Archipelago (John Rooney, pers. comm., 2012) have revealed extensive mesophotic coral reef ecosystems with diverse reef-building coral species. While classically considered to be limited to 100 m, mesophotic reefs have been observed as deep as 130 m in some of these areas, including at depths in excess of 150 m in the Auʻau Channel of Hawaii (Blythe-Skyrme et al. 2013). Likewise, investigations on Australia's GBR found extensive mesophotic habitats both along the continental shelf-edge and on submerged reefs inside the lagoon of the GBR, both of which support previously unknown communities of reef-building corals (Bridge et al. 2012a, Bridge et al. 2012b, Bridge and Guinotte 2013; Muir et al. 2018). These studies expand the known potential habitats for reef-building corals, but species diversity and abundances have not been well documented due to the relative inaccessibility of these habitats to divers.

2.2.3.   Spatial and Temporal Refugia

The above information on Habitat Diversity illustrates the enormous heterogeneity of the environments that Indo-Pacific reef-building corals inhabit. Each species occurs in a patchwork of habitat conditions that may vary over time in different ways, including cyclically (e.g., from tidal, seasonal, annual, and decadal cycles), episodically (e.g., storms, temperature anomalies, etc.), and linearly (e.g., gradual thermal regime changes). The dynamic nature of reef-building

coral habitats may provide refugia for some corals from some threats, such as ocean warming, both spatially and temporally (Riegl and Piller 2003, McClanahan et al. 2011, Fine et al. 2013).

Some habitats have natural features that reduce stress from extremely high temperatures or light levels, the most common causes of coral bleaching, and may provide spatial refugia for some reef-building coral species from ocean warming and other threats. For instance, deeper (mesophotic) habitat may be cooler depending on the amount of mixing, and it is exposed to less light. Mesophotic habitats are extensive throughout the Indo-Pacific, and there is some evidence that they function as refugia for some reef-building corals. A review of mesophotic habitat on Australia's GBR concluded that reef-building corals in mesophotic habitat are less likely to be affected by warming-induced bleaching events than their counterparts on nearby shallow reefs (Bridge et al. 2012b). Mesophotic habitat may also be important for recovery of disturbed coral reefs by providing sources of propagules to recolonize shallow reefs following disturbances (Bridge and Guinotte 2013). As stated earlier in 2.1.6, a 37-year record from the eastern Pacific across the two most severe El Niño events on record (1982–83 and 1997–98) shows how the thermally-sensitive reef-building fire coral, *M. intricata*, twice survived catastrophic bleaching in a deeper water refuge (>11 m depth). During both events, *M. intricata* was extirpated across its range in shallow water but showed recovery within several years, while two other fire corals without deep-water populations were driven to regional extinction (Smith et al. 2014). The refuge value of mesophotic habitats is limited by the fact that only about one-quarter of all reef-building coral species occur at mesophotic depths (Bongaerts et al. 2012), and evidence from the 2014-17 bleaching events suggests that mesophotic depths provides little to no refugia (Venegas et al. 2019).

Marginal habitats are also extensive, and in some cases function as refugia for some reef-building corals from some threats. Marginal habitats include turbid (Browne et al. 2012, Blakeway et al. 2013), very warm (Riegl et al. 2011, Riegl and Purkis 2012) or cold waters (Lybolt et al. 2011, Dalton and Roff 2013), soft substrates, and other environments with sub-optimal coral growth conditions (Done 1982, Perry and Larcombe 2003, Couce et al. 2012). A study of future coral habitat suitability under ocean warming and acidification suggests that marginal habitats may provide important refugia for some reef-building corals (Couce et al. 2013), though not all coral species can survive in these habitats. The study found that future climate change is likely to result in (1) range expansion at the high-latitude boundaries; (2) no decreased suitability in currently marginal eastern Equatorial Pacific locations as well as in the Atlantic generally; and (3) severe temperature-driven impacts in the western Equatorial Pacific (Coral Triangle) and surrounding regions. These findings led to the conclusion that marginal habitat is likely to function as a patchwork of refuge habitats for some reef-building corals in both the Indo-Pacific and Atlantic as ocean warming and acidification increase over the 21st century (Couce et al. 2013).

Aside from mesophotic and marginal habitats, other types of habitats may provide refuge for reef-building corals from ocean warming and other threats. Some of these have long been known to reduce thermal stress, such as those habitats with highly-fluctuating conditions, strong currents from wind or tides, and shading from frequent cloud cover or complex bathymetry (NMFS 2014). Unfortunately, some of these protective conditions may break down as oceans warm (Ainsworth et al. 2016). Other oceanographic features may also provide refugia from ocean warming, such as (1) Large-scale upwelling (Karnauskas and Cohen 2012); (2) the similar but smaller-scale phenomenon of internal tidal bores that transport cooler, deeper water to warmer, shallower areas (Storlazzi et al. 2013); and (3) wakes of relatively cool water left by the

passage of tropical cyclones (Carrigan 2012). Most of the refugia described above are with regard to ocean warming, but some of these habitat types provide refugia potential from ocean acidification, such as highly-fluctuating habitats which limit pH minima via tidal flux (Shaw et al. 2012a), and from disease and sedimentation, such as high-energy habitats which provide flushing that reduces conditions conducive to disease and removes sediment. Seagrass beds provide beneficial changes in ocean chemistry to seawater on adjacent reefs, providing local refugia from ocean acidification (Manzello et al. 2012). Many Indo-Pacific reef corals show habitat preferences for the mid to lower reef slope below 10 m depth, with depth thus providing refuge potential for these species (DeVantier and Turak 2017).

Thermal regime changes from ocean warming will have differing effects on habitat, depending on location. In locations already near the thermal maxima of reef-building corals, warming will degrade habitat, but in locations currently too cool for these species, warming may improve habitat, assuming other habitat features conducive to reef growth are also present such as hard substrate and appropriate light and water chemistry conditions. Geological evidence from past global warming periods shows a pattern of poleward expansion of some reef-building coral ranges, resulting in decline in equatorial areas (Kiessling et al. 2012) and expansion into temperate areas (Woodroffe et al. 2010). Predicted ocean warming in the twenty-first century is expected to result in a similar pattern of poleward expansion, thus newly-colonized areas may provide refugia for some species. For example, models suggest that such expansion of reef-building corals could occur at the rate of 1 – 4 km per year in Japan (Yara et al. 2011). However, these refugia are unlikely to be permanent because of the projected rapid worsening of ocean acidification at those latitudes (van Hooidonk et al. 2013, 2014).

As temperatures increase to the optimal range for reef-building corals in some northerly and southerly areas, these areas may become better habitat; however, a simultaneous increase in ocean acidification may negate the suitability of these areas (Yara et al. 2012, van Hooidonk et al. 2013, 2014). While there may be few long-term, large-scale refugia from both ocean warming and ocean acidification, on a finer regional or reef scales, there are still likely to be many small-scale refuges in the form of heterogeneous habitat, including non-reef and mesophotic habitats.

3. Key Trends in Indo-Pacific Reef-building Coral Communities

The health of reef-building coral communities is largely determined by the extent of disturbance, together with recovery from it. The most common measure of the status of Indo-Pacific reef-building corals is live coral cover. Resilience is the capacity of a community to recover from disturbance. Disturbance, recovery, coral cover, and resilience of Indo-Pacific reef-building coral communities on shallow coral reefs (i.e., coral reefs <30-40 m depth, not including non-reef and mesophotic areas) are described below, leading to some conclusions about trends in anthropogenic disturbance, the amount of time available for recovery from disturbance, live coral cover, and overall resilience. These trends are described both in terms of observations since relevant scientific information became available (≈1950), and projections over the foreseeable future (i.e., from now to 2100) under conditions projected for the 21st century in response to climate chang.

3.1. Disturbance

Disturbance is defined as an anthropogenic or natural event that results in large-scale coral colony mortality. All of the threats described in the Threats Evaluation below are at least partially anthropogenic, and have the potential to cause large-scale disturbance. Disturbances may be acute (shorter-term, more intense) or chronic (longer-term, less intense) (Connell 1997).

Natural disturbance is key for maintaining high diversity of reef-building corals in coral reef ecosystems. That is, over a given time period, variable conditions throughout cycles of disturbance and recovery at a given reef site enable a higher diversity of species to occur at that site than in the absence of disturbance (Hughes and Connell 1999). Observed and projected disturbance of Indo-Pacific reef-building coral communities is described below.

Observed Disturbance. Overall, observed acute and chronic disturbances of Indo-Pacific coral reefs have sharply increased over the past several decades (Birkeland 2019, Brainard et al. 2011). As described in the Ocean Warming section of the Threats Evaluation, the most important pattern in observed disturbance of Indo-Pacific coral reefs is the increase in the frequency, intensity, and magnitude of large-scale, warming-induced coral bleaching events. The repeated bleachings of 2014 – 2017 together constitute the most severe coral bleaching event ever recorded in the Indo-Pacific, and affected many remote reefs far from local human impacts (Eakin et al. 2017, Hughes et al. 2017a, Hughes et al. 2018a, Rodgers et al. 2017). There is not strong evidence that other types of acute disturbances have been increasing, such as predator outbreaks and tropical storms (Pratchett et al. 2014, IPCC 2013). Ocean acidification represents a chronic disturbance because of its continual effects on both coral calcification and reef accretion, and it has been observed to be increasing in the Indo-Pacific (Steiner et al. 2018). Localized chronic disturbances such as land-based sources of pollution (Prouty et al. 2014) are broadening and worsening on coral reefs near human populations throughout the Indo-Pacific.

Birkeland (2019) identified six ways that anthropogenic disturbances are affecting Indo-Pacific coral reefs: (1) Disturbance is nearly always faster than recovery; (2) damaged or stressed corals tend to produce fewer larvae; (3) reef community recovery times become longer when fast-growing branching corals are more vulnerable to stresses and disturbances, and are replaced by more tolerant slow-growing corals; (4) disturbances are becoming more frequent and do not allow sufficient time for recovery; (5) combinations of local and global disturbances and stresses result in positive feedbacks that accelerate reef degradation; and (6) degraded reefs decrease the proportion of habitat acceptable to recruiting larvae. As described above in the Habitat section, habitat heterogeneity and refugia produce a patchy mosaic of conditions across Indo-Pacific coral reefs, resulting in less exposure to disturbance in some locations. Consequently, there are typically areas, habitats, and micro-environments that are unaffected or less affected by even the most severe disturbances. For example, an analysis of heat stress patterns across the world between 1985 and 2012 showed very high spatial variability in the Indian Ocean and Australia, suggesting that some reefs in these areas were consistently less affected by bleaching than others (Heron et al. 2016). And although the 2014-2017 bleaching event was the worst on record in the Indo-Pacific, some areas such as Palau escaped relatively unscathed (Colin 2018).

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

3.2. Recovery

Recovery is defined as the restoration after a disturbance of an ecological community to a degree comparable to its original state (Pearson 1981). For the purposes of quantitatively comparing case studies of reef-building coral recovery, Connell (1997) defined "ecological significant recovery" as when the degree of recovery exceeds 50%, calculated as the ratio of the post-disturbance rise in coral cover compared to the amount that it had fallen in response to the disturbance. For example, if coral cover falls from 30% to 10% after a disturbance (20% fall), and subsequently rises from 10% to 25% (15% rise), then the degree of recovery is calculated by dividing the 15% rise by the 20% fall, giving 0.75 or 75%, which meets the definition of "ecological significant recovery" (Connell 1997). A higher level of recovery could be defined as approaching or attaining pre-disturbance coral cover at a site, while the highest level of recovery would be attaining pre-disturbance coral cover and community composition (i.e., species diversity of the community). Shorter periods of time are required for recovery of coral cover alone, as fast-growing reef-building coral species may be able to increase coral cover to pre-disturbance levels relatively quickly; however, this type of recovery typically results in a less diverse coral community with fewer slow-growing reef-building coral species than pre-disturbance (Berumen and Pratchett 2006, Birkeland 2019). As the rapidly-growing species are often more vulnerable, early successional stage coral reefs may lack the resilience of more diverse reefs. Most of the available information on observed Indo-Pacific coral reef recovery is in terms of coral cover only, but some is also in terms of community composition. Observed and projected recovery of Indo-Pacific reef-building coral communities are described below.

Observed Recovery. A review of responses to various types of disturbance at 35 Indo-Pacific coral reef sites from 1965 to 1990, based on the "ecological significant recovery" standard above, found that 29 were "significantly affected" (i.e., coral cover reduced by more than one-third by initial disturbance), of which 19 achieved ecological significant recovery, and 10 did not recover. All 35 sites were in the central and western Pacific portion of the Indo-Pacific. Of the sites that achieved significant recovery, most were affected by acute disturbances, whereas most of the sites that did not recover were affected by chronic disturbances (Table 1a; Connell 1997). A separate review of responses to bleaching only (i.e., all acute disturbances) at 98 Indo-Pacific coral reef sites from 1979 to 2006 included adequate data from 56 sites to apply the "ecological significant recovery" standard above. Of the 56 sites, 39 were "significantly affected" as defined above, of which 11 achieved ecological significant recovery and 28 did not. Of the sites that achieved significant recovery, most were in the central and western Pacific and Indian Oceans, whereas most of the sites that did not were in the eastern Pacific (Table 1b)(Baker et al. 2008).

Table 1a and 1b. <u>Recovery Results from 91 Indo-Pacific Coral Reef Sites, 1965-2006</u>: Responses to disturbance at 35 sites reviewed by Connell (1997)(Table 1a), and at 56 sites reviewed by Baker et al. (2008)(Table 1b).

1a. Connell (1997), 35 sites, 1965 – 1990.	Sites	Time (Yrs)	Disturbance types. All sites in Central & Western Pacific.
Significantly affected and recovered	19 (54%)	1-14	11 acute (storms, bleaching, predation, sediment, exposure), 8 chronic (sewage)
Significantly affected but not recovered	10 (29%)	4-21	3 acute (storm + exposure, bleaching, storm) 7 chronic (storms, sewage, oil spill)
Not significantly affected	6 (17%)	7-14	3 acute (storms, bleaching) 3 chronic (sewage)

1b. Baker et al. (2008), 56 sites, 1979 – 2006.	Sites	Time (Yrs)	All disturbance acute (bleaching). Sites in Central & Western Pacific (19), Indian Ocean (19), and Eastern Pacific (18)
Significantly affected and recovered	11 (20%)	4-23	6 sites in Central & Western Pacific, 3 in Indian Ocean, 2 in Eastern Pacific.
Significantly affected but not recovered	28 (50%)	3-20	3 sites in Central & Western Pacific, 11 in Indian Ocean, 14 in Eastern Pacific
Not significantly affected	17 (30%)	1-13	10 sites in Central & Western Pacific, 5 in Indian Ocean, 2 in Eastern Pacific

At the 30 sites that achieved ecological significant recovery in the two studies combined, most recovery was due to rapid regrowth of fast-growing branching or tabletop *Acropora* species. As stated above, recovery of a diverse coral community structure takes longer than recovery of coral cover alone because slower-growing reef coral functional groups need more time to become established. Most studies of recovery of coral cover and community structure have concluded that recovery from an acute disturbance usually takes about 10 – 15 years, as long as there are no additional chronic or acute disturbances (Birkeland 2019).

A total of 38 sites from the two studies that were significantly affected by disturbance did not achieve ecological significant recovery. Most of these were either exposed to chronic disturbance or repeated acute disturbances. A much higher proportion of eastern Pacific sites did not achieve ecological significant recovery (14/18 = 78%) than central and western Pacific and Indian Ocean sites (14/38 = 37%; Table 1b). The eastern Pacific includes eight of Veron's 133 Indo-Pacific ecoregions, and <50 of the Indo-Pacific's reef-building coral species (Veron et al. 2015). This area is subject to extreme temperature variability from the combined effects of strong upwelling (cold temperatures) and El Niño events (high temperatures), low aragonite saturation state, and frequent storms. Eastern Pacific reef-building corals have been among the slowest in the world to recover after disturbance (Brainard et al. 2011). Therefore, it is expected that a higher proportion of eastern Pacific sites would not recover than sites from elsewhere in the Indo-Pacific.

A total of 23 sites from the two studies were "not significantly affected" (Tables 1a and 1b). The threshold for "not significantly affected" was reduction in coral cover of less than one-third by the initial disturbance. If a threshold of <10% reduction in coral cover were to be used, then only 13 of the 91 sites would have been "not significantly affected." Regardless of which threshold is used, such sites where natural physical or biological conditions minimize warming-induced coral bleaching and mortality have "resistance" to bleaching (West and Salm 2003). The concept of resistance is important to resilience, and is discussed below in the Resilience section. Combining the results from both studies for the central and western Pacific and Indian Oceans

(35 sites from Connell 1997, plus 38 sites from Baker et al. 2008 = 73 sites), a total of 67% of the sites (49/73) achieved ecological significant recovery or were resistant (Tables 1a and 1b).

Writing about anthropogenic disturbance, Pearson (1981) predicted that "full recovery may be prolonged or prevented altogether because of permanent change to the environment, or a continuation of chronic, low-level disturbances." Indeed, the higher levels of anthropogenic disturbance across the Indo-Pacific over the last several decades may be reducing the proportion of sites that have the capacity to recover (Birkeland 2019), but there is inadequate information to determine if that is the case. In contrast, the increasing frequency of disturbance has clearly reduced the amount of time available for Indo-Pacific coral reefs to recover (recovery time). That is, the frequency of acute disturbances, together with ongoing chronic disturbances in many areas, has worsened over the last few decades to the point that neither coral cover nor community structure have adequate recovery time between disturbances on many reefs (Hughes et al. 2018b, Ortiz et al. 2018, Yadav et al. 2018). On the other hand, several characteristics of Indo-Pacific coral reefs result in reef-building coral communities being relatively less exposed to disturbance or more tolerant of it, as described in more detail in the Resilience section below.

Projected Recovery. As described in more detail in the Threats Analysis, all threats are projected to increase in the foreseeable future, especially under conditions projected for the 21st century in response to climate change, leading to higher frequency, intensity, and magnitude of both acute and chronic anthropogenic disturbances of Indo-Pacific coral reefs. One of the most important implications of the projected increasing frequency of disturbance is the subsequent reduction in recovery time. For example, an analysis of the timing of Annual Severe Bleaching (ASB) of the world's coral reefs in the 21st century concluded that ASB will occur on >75% of all reefs by mid-century, essentially eliminating the time available for recovery on those reefs (van Hooidonk et al. 2016). Although the spatial variability of conditions on Indo-Pacific coral reefs provides networks of refugia from threats, the increasing prevalence of all types of disturbance will likely erode or eliminate many of these refugia. Thus, the ever-increasing frequency of disturbance is projected to reduce the capacity of coral reefs to recover through reduction of recovery times (Hoegh-Guldberg et al. 2017, Hughes et al. 2017b, Torda et al. 2018), especially under conditions projected for the 21st century in response to climate change (Heron et al. 2017, van Hooidonk et al. 2016).

3.3. Coral Cover

Coral cover is defined as the percentage of the seafloor occupied by living reef-building corals, and is an important metric of coral reef health. Higher coral cover is typically correlated with higher fish and invertebrate diversity and abundance (Jones et al. 2004, Dustan et al. 2013), whereas lower coral cover is typically correlated with more bioerosion and loss of the reef framework (Perry et al. 2013, Kuffner and Toth 2016). Observed and projected coral cover on shallow Indo-Pacific coral reefs (i.e., <30-40 m, not including non-reef and mesophotic areas) is described below.

Observed Coral Cover. Current information on Indo-Pacific reef-building coral cover can be divided into four phases: (1) qualitative information based on historical photos and reconstructions, the region's first coral transect, and anecdotal accounts (late 19th to mid-20th centuries); (2) short-term, quantitative surveys on island to archipelagic scales (1966 – 1981); (3) long-term, quantitative analyses and surveys on archipelagic and regional scales (1977 – 2016); and (4) quantitative surveys of the immediate effects of the bleaching event of 2014-2017 on coral cover. Results from these four phases are described below. Coral cover varies naturally by latitude, reef type (fringing, atoll, barrier), habitat (backreef, lagoon, reef slope), depth, and other

natural variables, as well as by proximity to human populations, potentially confounding comparisons between locations or trends through time. This variability should be kept in mind when interpreting the following descriptions of coral cover in the four phases.

Observed Coral Cover - Phase 1. Historical photographs of emergent reef flat communities (i.e., exposed to air at low tide) on nearshore reefs within the central GBR show changes from high *Acropora* coral cover in 1890 to nearly zero coral cover in 2012 (Clark et al. 2012). A historical reconstruction of a nearshore reef slope at 5 m depth on the central GBR also shows that the *Acropora*-dominated coral community collapsed between 1920 and 1955, although coral cover eventually recovered via a *Pavona*-dominated community (Roff et al. 2013). Such massive losses of coral cover over the past century are common on many of the GBR's nearshore reef flats and reef slopes, as they have become covered with sediment and macroalgae from land-based sources of pollution (Hughes et al. 2010). In Pago Pago Harbor in American Samoa, the 247 m Aua Transect was established in 1917 across a reef flat from shore to the reef crest for one of the first studies of Indo-Pacific reef-building corals. In 1917, abundant corals were recorded along the entire transect, but between the 1950s and 1970s corals had nearly disappeared from the transect due to chronic pollution and coastal development in the harbor. In response to harbor clean-up by the early 1990s, some coral recovery occurred on the reef crest and outer fringe of the reef flat, but not on the majority of the transect (Fenner et al. 2013, Birkeland et al. 2013).

A collection of anecdotal accounts by early coral reef researchers describes high coral cover on reef flats and reef slopes in French Polynesia, the GBR, Thailand, Madagascar, east Africa, and the eastern Pacific from the 1950s to the 1970s. The qualitative descriptions and photos of reef slope coral communities are among the first made by scientists using scuba gear and underwater cameras in the Indo-Pacific, and are a testament to how much coral reefs have declined since the 1950s (Sale and Szmant 2012). This historical information on coral cover highlights the importance of the "shifting baseline syndrome" (Hughes et al. 2011), whereby our current perception is biased by a lack of long-term baselines prior to anthropogenic impacts. Anthropogenic disturbance resulted in coral cover declines long before modern monitoring programs began around 1980 (Phase 3 – see below), and prior to more recent threats such as warming-induced bleaching and ocean acidification (Pandolfi et al. 2003).

Observed Coral Cover - Phase 2. In the 1960s, researchers started collecting coral cover data, providing the first quantitative descriptions of coral cover on reef slopes of the Indo-Pacific. Archipelagic-scale or other large-scale reef slope surveys were conducted in the Philippines (Gomez et al. 1981), the Chagos Islands (Sheppard 1980), and the GBR (Endean and Stablum 1973). In addition, smaller-scale reef slope surveys were conducted, including at Fanning Island in Kiribati (Maragos 1974), at Pombo Island in Indonesia (Sumadhiharga 1977), at Koh Phuket in Thailand (Ditlev 1978), and in Guam (Randall 1973). The surveys had mean coral cover on reef slopes of 38% to 75% (Table 2). Even though all surveys were conducted on reef slopes, the results are not necessarily comparable to one another because they were collected at different latitudes, reef types, habitats, proximities to human populations, and depths, using different methods and personnel. However, they provide the first quantitative insight into historical coral cover on Indo-Pacific coral reefs.

These results are in general agreement with an expert opinion survey of 133 coral reef scientists around the globe to estimate coral cover based on earliest year of personal observations. The earliest year that a coral reef was observed ("earliest year observed") was listed as 1960 and the average was 1988. For the respondents around the globe whose earliest

year observed were in the 1970s, the mean estimate of baseline coral cover during those years was between 50 and 60% (Eddy et al. 2018). In comparison, for Indo-Pacific reef sites, the mean baseline coral cover estimates from 1966 - 1981 were 62% for the Indian Ocean and 61% for the Pacific Ocean (Table 2).

Table 2. <u>Coral Cover, 1966-1981</u>. Results from the first quantitative surveys of coral cover on Indo-Pacific coral reefs.

Location	Effort	Years	Reef type; habitat; depth	MCC (%)[*]	Notes
Guam (Randall 1973)	2 sites surveyed 1x/each	1966-1969	Fringing reef; shallow reef slope	54	Coral cover ranged from 40% to 60% on reef slope ("reef front" + "submarine terrace" zones).
GBR (Endean & Stablum 1973)	46 sites surveyed 1x/each	1969-1971	Platform reefs; seaward reef slopes; <20 m	38	Coral cover ranged from 9% to 64%.
Kiribati (Maragos 1974)	1 site surveyed 1x	1972	Atoll; seaward reef slope, 8-26 m	75	100 m transect w/ 1 m quadrats from 8 to 36 m; coral cover averaged 75% at 8-26 m depth, 20% at 27-36 m depth, and 62% overall.
Indonesia (Sumad-hiharga 1977)	4 sites surveyed 1x/each	1975	Atoll; seaward reef slopes; 1-6 m	65	Coral cover ranged from 38% to 77%.
Thailand (Ditlev 1978)	3 sites surveyed 1x/each	1976	Fringing reef; reef slope; 0-4 m	47	Coral cover ranged from 20% to 60% on reef slope components of reef flat transects.
Philippines (Gomez et al. 1981)	619 sites surveyed 1x/each	1976-1981	Various reef types; mostly reef slopes; depth not reported	39	Coral cover ranged from 0% to 100%: ● 5.5% of sites = 75-100% cover; ● 24.5% sites = 50-74.9% cover ● 37.8% sites = 25-49.9% cover ● 32.3% sites = 0-24.9% cover.
Chagos (Sheppard 1980)	19 sites surveyed 1x/each	1978-1979	Atolls; seaward reef slopes, 5-25 m	68	Coral cover ranged from 55% to 80%.

*MCC = mean coral cover.

Observed Coral Cover - Phase 3. More extensive reef monitoring programs began in the late 1970s and spread throughout the region in the following decades, providing time-series of coral cover data from many locations that can provide insight on temporal trends. Surveys or large-scale analyses of pre-existing data were conducted over 18 to 30-year periods to estimate coral cover trends in the Indo-Pacific (Bruno and Selig 2007), the Indian Ocean (Atewerberhan et al. 2011), the GBR (De'ath et al. 2012), the Philippines (Magdaong et al. 2013), and the central Pacific (Moritz et al. 2018). Overall mean coral cover decreased over these time periods in four of the studies, and increased in one study (Table 3). In addition, three of the studies examined coral cover trends in regions within their study areas, and found that regional mean coral cover decreased in eight of ten regions (Bruno and Selig 2007), seven of ten regions (Antewerberhan et al. 2011), and two of three regions (De'ath et al. 2012). Moritz et al. (2018) provided mean coral cover trend data for 19 countries or jurisdictions, finding increases in seven, decreases in five, and no trend in seven. Magdaong et al. (2013) did not sub-divide their study area, but rather examined coral cover trends inside and outside of MPAs, finding that those inside increased more than those outside.

Atewerberhan et al. (2011) documented a steady recovery in mean coral cover in the Indian Ocean over several years following the 1998 bleaching event. Other information from smaller-scale surveys corroborates this recovery. In the eastern Indian Ocean, annual surveys of 160 sites in seven countries showed a steady increase in mean coral cover from approximately 20% in 2005 to >40% in early 2016 (Gudka et al. 2018). In the Chagos Islands, surveys of 15 sites on four atolls showed an increase in mean coral cover from approximately 15% in 1999 to 30% in 2015 (Sheppard et al. 2017). Likewise, on the GBR, surveys of 243 sites showed an increase in mean coral cover from approximately 11% in 2012 to 24% in 2016 (AIMS 2017). However, all three studies reported sharp decreases in mean coral cover between early 2016 and late 2016 or 2017 in response to coral bleaching (AIMS 2017, Gudka et al. 2018, Sheppard et al. 2017).

Table 3 summarizes the best available information on mean coral cover trends over a four-decade period in the Indo-Pacific, providing insight into changes in coral cover in this vast area. In addition, the information from Phase 3 can be qualitatively compared to information from Phase 1 and Phase 2 to avoid "shifting baseline syndrome." As explained in the Phase 1 and Phase 2 sections above and illustrated in Table 2 above, mean coral cover on Indo-Pacific reef slopes before the 1970s likely approached or exceeded 50%. But after the 1970s, mean coral cover had declined to 20 – 40% or less on most reefs, representing relative losses of approximately half of all reef-building corals on some reefs (Table 3). These trends do not include the sharp declines in coral cover in many parts of the Indo-Pacific resulting from the historic coral bleaching event of 2014-2017 described in Phase 4 below.

Table 3. <u>Cover Cover Trends, 1977-2016</u>: Results from analyses and surveys of coral cover on Indo-Pacific coral reefs, showing percentage relative change of mean coral cover (%RC-MCC)* over the years observed.

Location	Effort	Years	Reef type; habitat; depth	%RC-MCC*	Notes on observed trends in mean coral cover (MCC) during portions of the time period, and methodology used for this table.
Indian Ocean (Ateweberhan et al. 2011)	1,997 surveys of 366 sites	1977 - 2005	Mostly fringing reefs & atolls; mostly reef slopes; 90% sites 5-10 m	-17.9	MCC decreased from ≈40% in 1996 to ≈20% in 1998 in response to 1998 bleaching event, then increased to 30.7% in 2005.
Eastern Indian to Central Pacific (Bruno & Selig 2007)	6,001 surveys of 2,667 sites	1980/2 - 2003[1]	Various reef types; mostly reef slopes; 1-15 m	-48.0	MCC calculated for 1980-82 to 2003 based on a subset of 154 sites surveyed in 1980-82, and most of the 2,667 sites surveyed from 1983 to 2003 (Bruno and Selig 2007, p. 4).
Philippines (Magdaong et al. 2013)	1,096 surveys of 317 sites	1981 - 2010	Mostly fringing reefs & reef slopes; mostly 2-20 m	+27.6	MCC increased from 29% in 1981 to >40% in 1994-96, decreased to 30% in 1998 in response to 1998 bleaching event, then increased to 37% in 2010.
GBR (De'ath et al. 2012)	2,258 surveys of 214 sites	1985 - 2012	Platform reefs; reef slopes; 6-9 m	-50.7	MCC decreased from 28.0% in 1986 to ≈23% in 1990 in response to crown-of-thorns seastar outbreaks and storms, increased to ≈25% in 1996, then decreased to 13.8% in 2012.
Central Pacific (Moritz et al. 2018)	19,270 surveys (# sites not reported)	1999 - 2016	Mostly fringing reefs & atolls; mostly reef slopes; mostly 0-15 m	-12.5	MCC calculated for all surveys combined. MCC reported individually for each of the 19 jurisdictions in the report, as well as for each monitoring program in each jurisdiction.

* Percentage relative change of mean coral cover (%RC-MCC) calculated in two steps: (1) MCC in % at the start (A) and end (B) of the time period were used to calculate the % change in MCC (C) over the time period (A-B = C); and (2) the % change in MCC (C) was divided by MCC in % at the start (A) to calculate the percentage relative change of mean coral cover over the time period (C/A x 100 = %RC-MCC).

Observed Coral Cover - Phase 4. As described in the Ocean Warming section below, the bleaching events of 2014-17 was the longest, most widespread, and likely the most damaging disturbance of Indo-Pacific reef-building corals on record (Eakin 2017). In the Hawaiian archipelago, bleachings occurred in 2014 and 2015, resulting in extensive bleaching and mortality, and subsequent loss of coral cover. On the west coast of the Big Island of Hawaii, mean coral cover decreased from 37.1% in 2014 to 18.4% in 2016, based on data from eight sites (Kramer et al. 2016). Outside of Hawaii, the worst year for bleaching was 2016. In the eastern Indian Ocean, mean coral cover decreased from approximately 41% in early 2016 to 33% in 2017, based on data from 131 sites (Gudka et al. 2018). In the Maldives archipelago, mean coral cover decreased from 25.6% in early 2016 to 6.3% in late 2016, based on data from five sites (Perry and Morgan 2017). On the GBR, mean coral cover decreased from approximately 24% in early 2016 to 18% in early 2017, based on data from 243 sites (AIMS 2017). Bleaching occurred on the GBR again in 2017, causing additional declines in coral cover in the northern, central, and southern GBR, the first time that simultaneous declines had been observed in all three areas (AIMS 2018).

The reductions in coral cover were not universal in the region, nor are they necessarily permanent. In some other parts of the Indo-Pacific, bleaching and coral cover losses were minimal, such as in the northern Red Sea (Osman et al. 2018), Palau (Colin 2018), and inshore turbid reefs of the GBR (Morgan et al. 2018). As described in the Recovery section above, corals normally recover from bleaching events with increasing coral cover over subsequent years, as was observed in the Indian Ocean (Atewerbehan et al. 2011) and the central and western Pacific (Baker et al. 2008) after the 1998 bleaching event, the second worst coral bleaching on record after 2016. Thus, the sharp declines in coral cover observed during Phase 4 are not necessarily permanent, given adequate recovery time, which requires that they be relatively free of major disturbances for several years.

      Coral Cover vs. Coral Community Composition. As described in the Recovery section above, coral cover is the simplest measure of the condition of reef-building coral communities, but may overlook changes in coral community composition. On reefs where coral cover is currently similar to historic levels, the increased disturbances during the industrial era may have caused major changes in the reef coral community composition. For example, a historical reconstruction of an inshore GBR reef showed that the *Acropora* community collapsed between 1920 and 1955 in response to chronic increases in sediments and nutrients following European settlement around 1870. Eventually, the coral community recovered but *Pavona* species replaced the *Acropora* species as the dominant taxa (Roff et al. 2013).

      At the Aua Transect in American Samoa, the coral community on the reef crest and outer reef flat was dominated by a variety of *Acropora* species in 1917. In 2007, this zone of the transect had even higher coral density, but was almost completely made up of a single *Acropora* species, *A. nana* (Birkeland et al. 2013). A study of a Moorea reef documented how the *Acropora* community was decimated in 1981 by the crown-of-thorns seastar (COTS). Subsequently, *Pocillopora* species became dominant, and coral cover of the *Pocillopora*-dominated community in 2003 was slightly higher than that of the *Acropora*-dominated community in 1979 (Berumen and Pratchett 2006). These studies show the importance of considering coral community composition together with coral cover when assessing changes to coral reef communities, rather than coral cover alone. However, there is much more time-series historical data on coral cover than on community composition in the Indo-Pacific.

      <u>Projected Coral Cover</u>. As described in the Disturbance and Recovery sections above the frequency of all types of disturbance combined, including the most important threat of ocean warming and warming-induced bleaching, is projected to increase throughout the 21st century; and, as disturbance frequency increases, the amount of time available for recovery from disturbance will correspondingly decrease. Disturbance drives coral cover down, and recovery time is necessary to allow it to rebound. Thus as disturbance frequency increases and recovery time decreases, it is highly likely that the observed trend of decreasing coral cover will continue. Therefore, we project that coral cover of Indo-Pacific reef-building corals will decrease in the foreseeable future, especially under conditions projected for the 21st century in response to climate change.

3.4. Resilience

      Resilience is a broader concept than recovery and can be defined as the capacity of corals to respond to disturbance by maintaining their original state through disturbance, recovering from disturbance without undergoing a phase shift (i.e., transition from a coral-dominated system to an algae-dominated system), or reversing to their original state after a phase shift (NASEM 2018). Thus resilience has three major components: (1) Resistance, defined as the ability to be

unaffected or lightly affected by disturbance; (2) recovery, as defined above in the Recovery section; and (3) reversibility, defined as the ability to shift back to the original state after a phase shift. Resilience applies to the individual (colony), population, and community levels, here termed "overall resilience." Loss of resilience is indicated both by the inability to recover, leading to a phase shift, and the inability to reverse a phase shift. Such loss of resilience has been widely observed in Caribbean coral reefs but not in Indo-Pacific coral reefs, because (1) The Caribbean has inherent characteristics that provide relatively less resilience than the Indo-Pacific such as relatively small ecosystem size, lower fish and coral diversity, and lower abundances of herbivores; and (2) human impacts in the Caribbean are higher than in the Indo-Pacific, and have resulted in an advanced state of coral reef degradation, and imperiled the foundational reef-building coral species (Burke et al. 2011, Roff et al. 2015). Observed and projected overall resilience of Indo-Pacific reef-building corals is described below to characterize trends in resilience.

     <u>Observed Overall Resilience</u>. As described above, anthropogenic disturbance of Indo-Pacific reef-building corals has increased, the amount of time available to recover from these disturbances has decreased, and coral cover has decreased. In each case, these trends are expected to continue and worsen. While these trends have been testing the overall resilience of Indo-Pacific reef-building corals, several characteristics of their biology and habitat, together with their responses to disturbances so far, suggest that the resilience of these communities remains quite high: (1) Observed impacts of disturbances on corals have been highly spatially variable due to habitat heterogeneity and varied geographic patterns of marine heatwaves during past bleaching events; (2) factors that confer resilience have not declined (high habitat heterogeneity, large ecosystem size, high coral and reef fish species diversity); (3) observed responses of corals to disturbances indicate that most were either resistant or recovered; and (4) observed responses of corals to disturbances indicate that phase shifts have so far been either rare or reversed. These four points are explained below.

     First, as described in the Biology and Habitat sections above, Indo-Pacific reef coral species occur across large ranges with high levels of habitat heterogeneity. This enables a network of refugia from any individual disturbance, in which connectivity across large ranges can facilitate recovery. For example, a model of the GBR's 3,800 reefs showed that about 100 of them act as source reefs that can replenish the GBR after disturbances, because they are highly connected via ocean currents to the wider reef network, and they have a relatively low risk of exposure to disturbances such as COTS outbreaks, thus producing "systemic resilience" for the GBR (Hock et al. 2017). Furthermore, an analysis of 123 Indo-Pacific sites within degraded coral reef ecosystems found that 38 of the sites had positive trends for coral cover because of favorable physical, biological, or ecological conditions that minimized the impacts of disturbance, demonstrating high spatial variability in resilience even on degraded reefs (Guest et al., 2018). Finally, the patterns of heat stress during marine heatwaves is quite variable. Bleaching and mortality in different years have been influenced by climate and weather patterns, such as the differential bleaching patterns seen in the GBR during the back-to-back 2016 and 2017 bleaching events.

     Second, in addition to high habitat heterogeneity, Indo-Pacific reef-building coral ecosystems have several other characteristics that confer resilience, including large size, relatively high reef-building coral and reef fish diversity, and high resistance to algal dominance (Roff and Mumby 2012). None of the above factors that maintain resilience (high habitat heterogeneity, large ecosystem size, high coral species diversity, and high reef fish species

diversity) are in decline in the Indo-Pacific. However, loss of coral cover and diversity (and therefore habitat) through projected increase in disturbance may negatively affect each of these resilience characteristics.

Third, as described in the Recovery section above, reviews of the responses of Indo-Pacific reef-building corals to disturbance (Connell 1997, Baker et al. 2008) found that two-thirds of the sites in the central and western Pacific and Indian Oceans recovered from disturbance, or were resistant to it (49/73 sites = 67%; Tables 1a and 1b) during past events. The opposite was true for the eastern Pacific sites, where the majority (14/18 sites = 78%) did not recover. However, as also described in the Recovery section, the eastern Pacific is exposed to uniquely harsh conditions and represents very small proportions of the Indo-Pacific's ecoregions and reef-building coral biodiversity.

Fourth, observed responses of Indo-Pacific corals to disturbances indicate that, until recently, phase shifts have so far been either rare or reversed. While phase shifts have been documented in the Indo-Pacific in response to disturbance (Ledlie et al. 2007, Bozec et al. 2018), they have occurred on a small proportion of disturbed reefs, or have reversed to coral-dominated systems. For example, over a 15-year period of monitoring on 47 GBR reefs starting in the mid-1990s, during which time the reefs were subjected to multiple disturbances, only one reef underwent a coral–macroalgal phase shift (Cheal et al. 2010). In other cases where phase shifts have been observed, natural conditions following the phase shifts favored coral over algae, allowing for reversals (Graham et al. 2013). A more typical example of a coral community response to a disturbance is provided in Hawaii by the response to back-to-back bleaching events on the Big Island in 2014 and 2015, when reef-building corals suffered over 50% mortality by 2016 (Kramer et al. 2016). In the ensuing years (2016-2018), the remaining corals stabilized and started to recover, and algae did not become dominant (TNC 2019).

Projected Overall Resilience. While there are characteristics that lend some level of resilience to Indo-Pacific reef-building corals, the limits of this resilience are likely to be reached in the foreseeable future, even on remote reefs (Smith et al. 2017). As described in the Threats Evaluation, all major threats to Indo-Pacific reef-building corals are projected to increase throughout the 21st century, including the most important threat of ocean warming and warming-induced bleaching. Consequently, disturbance and bioerosion are projected to increase, and recovery times and coral cover are projected to decrease. Thus, the trajectory of overall resilience for Indo-Pacific reef-building coral colonies, populations, and communities is projected to decline in the foreseeable future (Birkeland 2019), especially under conditions projected for the 21st century in response to climate change.

3.5. Trends Conclusion

Disturbance, recovery, coral cover, and resilience of Indo-Pacific reef-building corals on shallow coral reefs (i.e., coral reefs <30-40 m depth, not including non-reef and mesophotic areas) are described above, both in terms of observations since relevant scientific information became available, and projections over the foreseeable future (i.e., from now to 2100) under conditions projected for the 21st century in response to climate change. This information leads to some conclusions about trends in anthropogenic disturbance, recovery time, coral cover, and overall resilience.

Anthropogenic Disturbance. The main threats to Indo-Pacific reef-building corals are anthropogenically driven, and most have been increasing over the last half-century or more. In particular, the most important threat, ocean warming, has resulted in increasing frequency, severity, and magnitude of marine heatwave impacts on coral reefs over the last several decades.

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Anthropogenic disturbance of Indo-Pacific reef-building corals is projected to increase even more in the foreseeable future, which will exacerbate ocean warming and other global threats, together with the growing human population which will exacerbate local threats (Table 4).

Recovery Time. Studies of the recovery of Indo-Pacific reef-building corals (excluding the eastern Pacific) show that the majority of sites showed significant recovery from, or resistance to, anthropogenic disturbance over the latter part of the 20th century and early part of the 21st century (Tables 1a and 1b). The available information does not indicate that the capacity for recovery of Indo-Pacific reef-building corals has substantially declined. However, due to increased frequency of disturbance, the amount of time available for corals to recover has declined. Furthermore, since the frequency of disturbance is projected to increase, especially under conditions projected for the 21st century in response to climate change, the time available for recovery between events is projected to continue to decrease in the foreseeable future (Table 4).

Coral Cover. The available information clearly indicates that mean coral cover has declined across much of the Indo-Pacific since the 1970s (Tables 2 and 3), and likely many decades before then in some locations. High spatial and temporal variability influenced by a large number of natural and anthropogenic factors can mask the overall trend in coral cover, but long-term monitoring programs and meta-analyses demonstrate downward temporal trends in most of the Indo-Pacific. Because disturbance is projected to increase in frequency in the foreseeable future and this is expected to result in reduced recovery times, mean coral cover in the Indo-Pacific is also projected to decrease (Table 4).

Overall Resilience. Despite increasing disturbance, decreasing recovery times, and decreasing coral cover, the available information suggests that overall resilience of Indo-Pacific reef-building corals so far remains quite high because: (1) observed impacts of disturbances on corals have been spatially highly variable due to habitat heterogeneity; (2) factors that confer resilience have not declined; (3) observed responses of corals to disturbances indicate that most either were resistant or recovered; (4) observed responses of corals to disturbances indicate that phase shifts have so far been either rare or reversed. However, the trends in disturbance, recovery time, and coral cover are projected to worsen, thus overall resilience is also projected to decrease in the foreseeable future (Table 4).

In summary, anthropogenic disturbance is expected to increase, while recovery time, coral cover, and overall resilience are all expected to decrease in the foreseeable future.

Table 4. Summary of Trends: Observed and projected trends in anthropogenic disturbance, time available for recovery, coral cover, and overall resilience of Indo-Pacific reef-building coral communities on shallow coral reefs (<30-40 m).

Key Trend	Observed*	Projected*
Anthropogenic Disturbance	↑	↑
Recovery Time	↓	↓
Coral Cover	↓	↓
Overall Resilience	O	↓

* Observed = from mid-20th century to present. Projected = from present to 2100. ↑ = a negative upward trend. ↓ = a negative downward trend. O = available information does not indicate any trend.

4. Threats Evaluation for Indo-Pacific Reef-building Corals

Section 4(a)(1) of the ESA and NMFS' implementing regulations (50 CFR 424) state that the agency must determine whether a species is endangered or threatened because of any one or more of the following five factors: (A) present or threatened destruction, modification, or curtailment of habitat or range; (B) overutilization for commercial, recreational, scientific, or educational purposes; (C) disease or predation; (D) inadequacy of existing regulatory mechanisms; or (E) other natural or manmade factors affecting its continued existence. Based on the 2011 SRR (Brainard et al., 2011), the 2014 final coral listing rule (NMFS 2014), and the information cited in the Threats Evaluation below, we have identified the eight most important threats to Indo-Pacific reef-building corals currently and in the foreseeable future: Ocean warming, ocean acidification, sea-level rise, fishing, land-based sources of pollution, coral disease, predation, and collection and trade. In addition, a group of less important threats, as well as the interactions of the most important threats, are also described. We related each threat to ESA Factors A, B, C, and E. Factor D is treated separately because it does not constitute a physical or biological condition that directly threatens reef-building corals, but rather consists of treaties, agreements, laws, and regulations (or lack thereof) at the international, national, state, and local level that may influence the direct threats.

Ocean warming, ocean acidification, and sea-level rise are all direct results of increased concentrations of atmospheric CO_2 and other greenhouse gases. Because of its prominent role in threatening reef-building corals, an overview of global climate change is provided at the beginning of the Threats Evaluation below in Section 4.1. This is followed by descriptions of each threat in Section 4.2, inadequacy of regulatory mechanisms in Section 4.3, and the Threats Evaluation conclusion in Section 4.4. Threats are described in terms of observed and projected effects to Indo-Pacific reef-building corals. "Observed" refers to the time period since relevant scientific information became available (usually mid-20th century), while "projected" refers to the time period between now and the year 2100.

4.1. Global Climate Change

Some of the most important threats contributing to the extinction risk of Indo-Pacific reef-building corals are related to global climate change. Global climate change refers to increased concentrations of greenhouse gases (GHGs; carbon dioxide, methane, nitrous oxide, and others, of which carbon dioxide makes up approximately 80% of the total) in the atmosphere from anthropogenic emissions, and subsequent warming of the earth, acidification of the oceans, rising sea-levels, and other impacts since the beginning of the industrial era (starting in the mid-19th century). Since that time, the release of carbon dioxide (CO_2) from industrial and agricultural activities has resulted in atmospheric CO_2 concentrations that have increased from approximately 280 ppm in 1850 to 410 ppm in 2018. The resulting warming of the earth has been unequivocal, and each of the last three decades has been successively warmer than any preceding decade since 1850. The climate change components of this status assessment are based on the International Panel on Climate Change's (IPCC) Fifth Assessment Report "Climate Change 2013: The Physical Science Basis" (AR5; IPCC 2013), the IPCC's "Global Warming of 1.5° C" (1.5° Report; IPCC 2018), and other climate change literature cited below. The IPCC published the 1.5° Report to compare the impacts of global warming of 1.5° C vs. 2.0° C above pre-industrial levels, in response to the 2015 Paris Agreement's objective of limiting global warming to 1.5° C. The IPCC's AR5 and the 1.5° Report together represent the largest synthesis of global climate change physical science ever compiled. The IPCC is currently compiling its Sixth Assessment Report (AR6), due out in 2021 or 2022.

Based on the two IPCC reports mentioned above, this introduction to global climate change covers (1) an overview of observed and projected global mean surface temperatures (GMST) from the pre-industrial baseline period of 1850-1900 to the year 2100; (2) the IPCC's pathways for projecting climate change, including GMSTs, from now to the year 2100; (3) why we use the time period from now to the year 2100 as "the foreseeable future" for analyzing climate change-related threats in this assessment; and (4) why we use the IPCC's Representative Concentration Pathway 8.5 for analyzing climate change-related threats in this assessment. This introduction provides context for the global climate change-related threats of ocean warming, ocean acidification, and sea-level rise described in the following Threats Evaluation.

Observed and Projected GMSTs, 1850 – 2100. GMST refers to the mean of air temperatures observed at the earth's surface over both land and sea. GMSTs can be calculated for the period of 1850 to 1900 based on temperature data collected from around the world by the United Kingdom's Hadley Centre and the University of East Anglia's Climatic Research Unit, known as HadCRUT. Data from this period is used to establish the "pre-industrial" GMST baseline that the IPCC compares with subsequent temperature changes (Fig. 2). According to the HadCRUT data, between the pre-industrial period and the decade 2006–2015, observed GMST increased by 0.87° C (1.57° F). Estimated anthropogenic global warming matches the level of observed warming to within ±20%. Estimated anthropogenic global warming is currently increasing at 0.2° C (0.36°F) per decade due to past and ongoing GHG emissions. Warming greater than the global annual average is being experienced in many land regions and seasons, including two to three times higher in the Arctic. Warming is generally higher over land than over the ocean, thus warming of the ocean lags behind warming of air at the earth's surface. Regardless of future emissions, warming from past anthropogenic GHG emissions since the pre-industrial period will persist for centuries to millennia, and will continue to cause further long-term changes in the climate system, such as sea-level rise, with associated impacts (IPCC 2013, IPCC 2018).

AR5 (IPCC 2013) projected GMST from 2006 over the remainder of the 21st century using a set of four Representative Concentration Pathways (RCPs) that provide a standard framework for consistently modeling future climate change under different assumptions. The four RCPs span a range of possible futures, from high GHG emissions peaking near 2100 (RCP8.5), to intermediate emissions (RCP6.0 and RCP4.5), to low emissions (RCP2.6). The projected effects of RCP8.5 and RCP2.6 on GMST through the 21st century are shown in Figure 2. RCP2.6 still results in nearly 2° C (3.6°F) increase in GMST during the 21st century above pre-industrial levels. The 1.5° Report (IPCC 2018) was written to compare the impacts of global warming of 1.5° C (2.7°F) vs. 2.0° C above pre-industrial levels, in response to the 2015 Paris Agreement's objective of limiting global warming to 1.5° C. In order to do this, it was necessary to create new pathways to reflect the massive cuts in GHG emissions needed to accomplish the ambitious objective. The basis for the IPCC's pathways is described in more detail below.
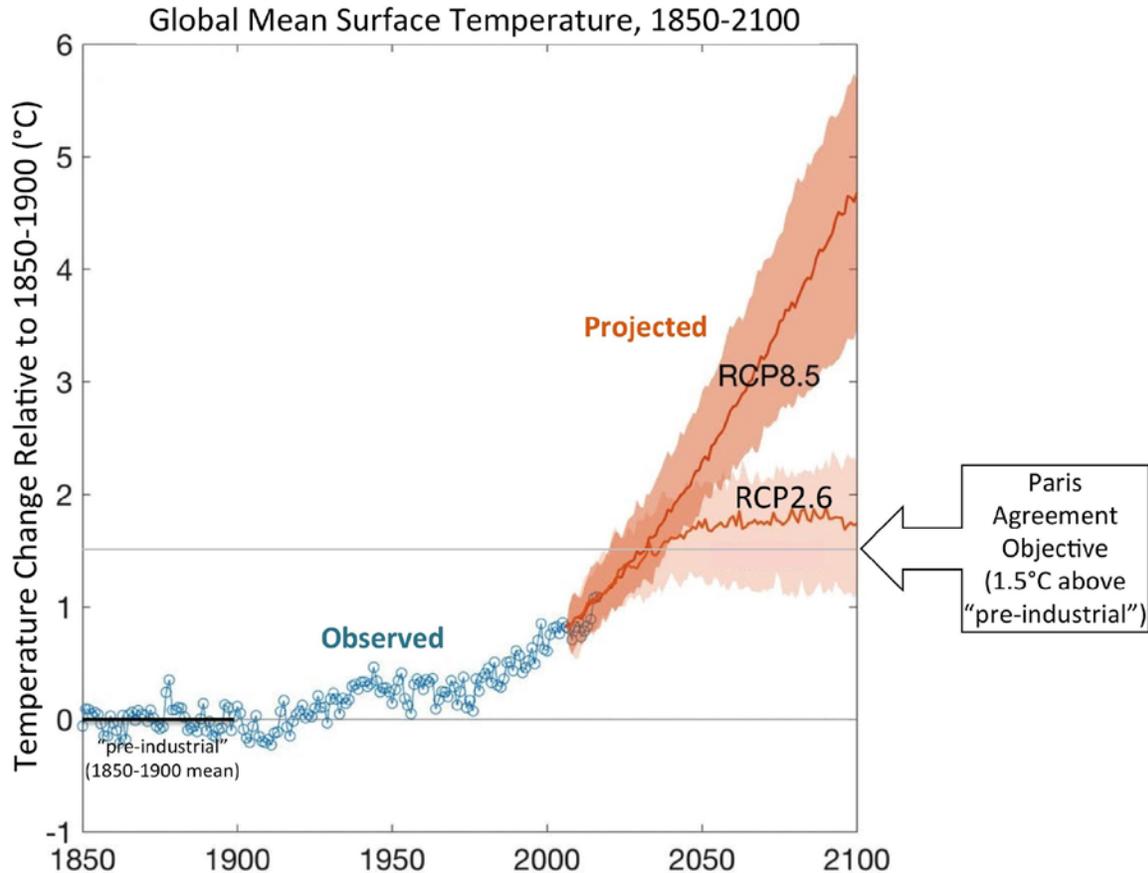
Figure 2. <u>Global Mean Surface Temperature (GMST), 1850-2100</u>: Observed vs. projected GMST from 1850 to 2100 relative to pre-industrial. Projected temperatures are shown for RCPs 8.5 vs. 2.6 with error bands (Henley and Abram 2017, IPCC 2013).

      <u>The RCPs for Projecting Climate Change to 2100</u>. As atmospheric GHG concentrations increase, less of the sun's heat can be radiated back into space, causing the earth to absorb more heat. The increased heat forces changes on the earth's climate system, and thus is referred to as "radiative forcing." AR5's four RCPs are named according to increases in radiative forcing of 2.6, 4.5, 6.0, and 8.5 Watts per square meter (W/m^2) of the earth's surface. These result from atmospheric CO_2 concentrations of 421 (RCP2.6), 538 (RCP4.5), 670 (RCP6.0), and 936 ppm (RCP 8.5) in 2100. The four pathways were developed with the intent of providing different potential climate change projections to guide policy discussions. The IPCC does not attach likelihoods to the pathways. Taken together, the four pathways project wide ranges of increases in GMSTs, ocean warming, ocean acidification, sea level rise, and other changes globally throughout the 21st century (IPCC 2013).

      Recently, there has been increasingly broad concern about the future impacts of all four AR5 pathways, and that even RCP2.6 could result in unprecedented and irreversible impacts to natural and social systems, including coral reefs. This concern led to the United Nations' Paris Agreement in 2015 (signed in 2016 by 195 countries), the objective of which is to limit GMST to 1.5° C above pre-industrial levels (UN 2016), which is only approximately 0.5° C (0.9°F) above

current GMST. Since not even RCP2.6 would limit GMST by 1.5° C above pre-industrial levels (see Fig. 2 above), it was necessary to develop a new models based on the atmospheric CO_2 concentration needed to meet this goal, as well as a plan for achieving it. Hence the 1.5° Report was commissioned in 2016 and completed in 2018 (IPCC 2018). The 1.5° Report uses a group of pathways with lower emissions than RCP2.6, which would result from an atmospheric CO_2 concentration of approximately 400 ppm, less than the 2018 level (≈410 ppm). Thus, successful implementation of the Paris Agreement would not only require an immediate and sharp decrease in global GHG emissions, but also CO_2 removal from the atmosphere (IPCC 2018). Together, AR5 and the 1.5° Report provide the pathways that the IPCC uses for projecting future climate change impacts on GMST, ocean warming, ocean acidification, and sea-level rise.

       The Foreseeable Future is From Now to 2100. The IPCC pathways (IPCC 2013, IPCC 2018) use the year 2100 as the main end-point (some models also go beyond 2100), and the 2014 final coral listing rule (NMFS 2014) defined the foreseeable future as the period of time from the present to the year 2100. That is, the foreseeable future is not defined as the year 2100, but rather as the time period from now to the year 2100, with increasing uncertainty in climate change projections over that time period. So while precise conditions during the year 2100 are not necessarily foreseeable, the general trends in conditions during the period of time from now to 2100 are reasonably foreseeable as a whole under the assumptions set for each of the pathways, although less so farther out in time. Because the time period from now to the year 2100 is strongly supported as a reasonably foreseeable timeframe in the climate science projections in AR5 (IPCC 2013) and the 1.5° Report (IPCC 2018), and because the climate-related impacts to coral reefs are likely to be severe within that timeframe for multiple climate change pathways, we find that the time period of the present to the year 2100 is the appropriate timeframe for purposes of analyzing climate change-related threats in this assessment.

       RCP8.5 is the Status Quo Pathway. Since AR5 was published in 2013, climate change science has continued to advance at a rapid pace, including in the 1.5° Report and the scientific literature. Summaries of the most recent information on observed and projected ocean warming, ocean acidification, and sea-level rise are provided below. With regard to projection of future climate change, the 2014 final coral listing rule (NMFS 2014) considered RCP8.5 to be the most likely future pathway, because observed growth in GHG emissions and atmospheric CO_2 concentrations over the years preceding the listing were more consistent with RCP8.5 since 2006 than any other pathway. The 2016 NMFS policy for ESA and climate change decisions (NMFS 2016) states that RCP8.5 should be considered the status quo climate change pathway.

       Recent GHG emissions and global atmospheric CO_2 concentrations continue to support this approach: According to the most recent Global Carbon Budget report (Friedlingstein et al 2019), global CO_2 emissions from fossil fuels and industry grew continuously from 2010 to 2019; and global atmospheric CO_2 concentration grew from approximately 385 to 410 ppm, with each year setting new historic highs, according to NOAA's Earth System Research Laboratory (ESRL) station on Mauna Kea, Hawaii (https://www.esrl.noaa.gov/gmd/ccgg/trends/, accessed December 2019). Thus, the best available current information continues to support the NMFS policy that RCP8.5 is the most representative pathway of the status quo among those used by the IPCC in AR5 (IPCC 2013) and the 1.5° Report (IPCC 2018). Because we consider RCP8.5 to be the status quo climate change pathway, we provide summaries of RCP8.5's projections over the foreseeable future for the climate change threats of ocean warming, ocean acidification, and sea-level rise below.

4.2. Most Important Threats to Indo-Pacific Reef-building Corals

The 2011 Status Review Report identified 19 threats to the world's reef-building corals (Brainard et al. 2011). Of those, we consider the global climate change-related threats of ocean warming, ocean acidification, and sea-level rise, and the local threats of fishing, land-based sources of pollution, coral disease, predation, and collection and trade to be the most important to the extinction risk of Indo-Pacific reef-building corals currently and in the foreseeable future, the most important of which is ocean warming. Several secondary global and local threats are also mentioned, as well as the interactions of the threats with one another. These threats are described in detail below.

4.2.1. Ocean Warming (ESA Factor E)

Ocean warming refers to the ongoing warming of the world's oceans from anthropogenic global climate change, and thus is considered under ESA Factor E – other natural or manmade factors affecting the continued existence of the species. Ocean warming results in warming-induced bleaching and mortality of corals, and is considered to be the most important threat to Indo-Pacific reef-building corals. To adequately describe this threat, we provide summaries of (1) observed ocean warming to date; (2) projected ocean warming in the foreseeable future (i.e., from now to 2100); (3) observed effects of warming-induced mass bleaching on Indo-Pacific reef coral communities to date; and (4) projected effects of warming-induced mass bleaching on Indo-Pacific reef coral communities in the foreseeable future.

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

In AR5, the IPCC estimated that the upper layer (0−700 m) of the world's oceans warmed from 1971 to 2010 by 0.11° C (0.20°F) per decade. Warming varied regionally among the oceans, but all oceans warmed between 1971 and 2010, including the tropical and sub-tropical Indo-Pacific (IPCC 2013). AR5 was based on data collected through 2010, but data collected by the NOAA National Centers for Environmental Information (NCEI) since then show a continued increase in mean global ocean temperatures from 2011 to 2017 (NCEI 2018). Indeed, there was a greater increase in ocean warming from 2014 to 2016 than any previous three-year period on record (Jewett and Romanou 2017). There is consensus among users of several different methods of monitoring seawater temperatures that ocean warming has continued unabated since 2010 both globally and regionally in all of the world's oceans (Gleckler et al. 2016, Wang et al. 2018). Between 1998 and 2015, the greatest warming was recorded in the Southern Ocean, the tropical/subtropical Pacific Ocean, and the tropical/subtropical Atlantic Ocean (Cheng, et al. 2017). This resulted in an increase in marine heatwaves (Oliver et al. 2018), including those that cause bleaching and death of corals.

Projected Ocean Warming. AR5's Annex 1, Supplementary Material for RCP8.5 (IPCC 2013) provides detailed projections of future warming of air over land and sea grid points of the earth's surface under RCP8.5 for the time periods 2016-2035, 2046-2065, and 2081-2100, including regional projections within the range of Indo-Pacific reef-building corals. Warming of

seawater at the sea's surface lags behind warming of air at the sea's surface. Although AR5's detailed projections in the Supplementary Materials are for air at the sea's surface, they indicate likely proportional warming of seawater (IPCC 2013). These projections provide the best available information on future global warming and subsequent future ocean warming within the range of Indo-Pacific reef-building corals, as described below.

Projected changes in Indo-Pacific mean annual air temperatures at the ocean surface compared to the 1986-2005 average are shown in the figures in AR5's Annex I, Supplementary Material for RCP8.5 for the West Indian Ocean, North Indian Ocean, Southeast Asia, North Australia, and Pacific Islands areas (IPCC 2013, Figures AI.SM8.5.92, 116, 124, 132, and 140). Based on the maps, the following approximate increases in air temperatures at the ocean surface are projected for all areas: For 2016-2035, 0.0-1.0° C (0.0-1.8°F); for 2046-2065, 1.0-3.0° C (1.8-5.4°F); and for 2081-2100, 2.0-5.0° C (3.6-9.0°F). Spatial variability in the projections consists mostly of larger increases in the Red Sea, Persian Gulf, and the Coral Triangle, and lower increases in the central and eastern Indian Ocean and south-central Pacific (IPCC 2013, Figures AI.SM8.5.92, 116, 124, 132, and 140). The ranges in the projections described above are from the maps and are for the 25% to 75% range, however ranges of projections within the 5% to 95% range are considerably greater (IPCC 2013).

We interpret these projections as follows: (1) Mean global ocean surface temperatures are likely to rise approximately 2-5° C by 2081-2100 under RCP8.5, greatly exacerbating the impacts of ocean warming on Indo-Pacific reef-building corals; (2) these mean projections are not necessarily representative of ocean surface temperature conditions throughout the ranges and habitats of Indo-Pacific reef-building corals due to spatial variability and statistical ranges; and (3) ocean surface temperature conditions are assumed to vary spatially at the larger spatial scales shown in AR5 for the Indo-Pacific areas, and more so at finer spatial scales.

Observed Effects of Warming-Induced Mass Coral Bleaching. While coral bleaching patterns are complex, there is general agreement that thermal stress has led to accelerated bleaching and mass mortality during the past several decades. During the years 1983, 1987, 1995, 1996, 1998, 2002, 2004, 2005, 2014, 2015, 2016, and 2017 widespread warming-induced coral bleaching and mortality was documented in many Indo-Pacific reef coral communities (Jokiel and Brown 2004, Kenyon and Brainard 2006, Brainard et al. 2011, Rodgers et al. 2017, Hughes et al. 2017a, 2018a). The series of coral bleachings in 2014-2017 are considered a single 3-year event by NOAA's Coral Reef Watch (Eakin 2017). It was the longest, most widespread, and likely the most damaging coral bleaching event on record. It affected more coral reefs than any previous global bleaching event, and was worse in some locales than ever recorded before (e.g., GBR). Heat stress during this event also caused mass bleaching in several reefs where bleaching had never been recorded before such as in the northernmost GBR and uninhabited atolls of the central Pacific (Bahr et al. 2015, Eakin et al. 2016, Couch et al. 2017, Eakin et al. 2017, Kayanne et al. 2017). In addition to these recent papers, the 4th National Climate Assessment by the U.S. Global Climate Research Program (USGCRP) concluded that it has "very high confidence" that disruption of coral reef ecosystems has already occurred due to ocean warming (USGCRP 2018). As described in the Trends section above, there clearly has been a long-term overall decline in coral cover in the Indo-Pacific, and these repeated warming-induced mass bleaching events correlate with the steepest declines in coral cover.

The 2014-2017 warming-induced bleaching across the Indo-Pacific was the worst in recorded history in terms of severity and duration of elevated seawater temperatures and ensuing mass coral bleaching and mortality (Lough et al. 2018). For example, much of the GBR was

affected by the elevated seawater temperatures, resulting in bleaching levels of 75-100% on many of the GBR's northern reefs, and a mean reduction in live coral cover of 30% across the entire 2,300 km GBR between March and November 2016 (Hughes et al. 2017a). The frequency, intensity, and magnitude of mass coral bleaching events in the Indo-Pacific have rapidly increased since the early 1980s, marking the transition to a new era in which the interval between recurrent bouts of coral bleaching is too short for a full recovery of mature assemblages (Hughes et al. 2018a), as also described in Trends section above.

The capacity of reef-building corals to acclimatize (i.e., the process by which an individual colony physiologically adjusts to changes in its environment) or adapt (i.e., the process by which a coral population genetically adjusts to changes in its environment) to warming seawater temperatures may have buffered some species or populations from the full effects of the above bleaching events. However, any such capacity is dependent on species, location, habitat type, and many other factors. The bleaching and mortality of some colonies of a coral species on a reef, followed by the recovery of hardier colonies, is the process by which acclimatization and adaptation of a species to ocean warming occurs. For example, in comparisons of 1998 and 2010 bleaching events and recovery in Southeast Asia, some coral species demonstrated more resistance to bleaching in 2010, suggesting acclimatization or adaptation to thermal stress (Sutthacheep et al. 2013). An analysis of observed versus predicted coral bleaching events suggests that corals may have already responded adaptively to some warming during the industrial era because observed bleaching responses are lower than predicted by the warm temperature anomalies (Logan et al. 2013). A study of a fast-growing, shallow water coral species demonstrated that acclimatization and adaptive responses allowed them to inhabit reef areas with water temperatures far above their expected tolerances (Palumbi et al. 2014). In the back-to-back bleachings on the GBR in 2016 and 2017, there was less bleaching in 2017 than in 2016, apparently because the 2016 survivors acclimatized to warmer conditions (Hughes et al. 2018c). There is a large body of literature on the acclimatization and adaptation capacities of reef-building corals to ocean warming (reviewed by Coles and Brown 2003, Putnam et al. 2017), much of which suggests some limited capacity.

As described in the Habitat section above, habitat heterogeneity can provide spatial and temporal refugia from the seawater temperature conditions that cause coral bleaching. Colony location can moderate exposure of colonies of the species to ocean warming by latitude or depth because colonies in higher latitudes and/or deeper areas are usually less affected by warming events. Mesophotic habitats are generally less affected because lower irradiance reduces the likelihood of warming-induced bleaching (Bridge et al. 2012b, Smith et al. 2014), although recent evidence from across the Pacific demonstrates that heat stress at depth can sometimes be similar to or even greater than at the surface (Venegas et al. 2019). Some locations are blocked from warm currents by bathymetric features, and some habitat types reduce the effects of warm water, such as highly fluctuating environments. Physical processes can moderate exposure of colonies of the species to ocean warming in many ways, including processes that increase mixing (e.g., wind, currents, tides), reduce seawater temperature (e.g., upwelling, runoff), or increase shading (e.g. turbidity, cloud cover). Documented refugia of reef corals from ocean warming include by depth (Smith et al. 2014), turbidity (Browne et al. 2012, Blakeway et al. 2013), upwelling (Karnauskas and Cohen 2012), tidal bores (Storlazzi et al. 2013), and the wakes of relatively cool water left by the passage of tropical cyclones (Carrigan 2012).

Projected Effects of Warming-Induced Mass Coral Bleaching. The responses of the world's corals and coral reef ecosystems to ocean warming and other threats in the foreseeable

future have been addressed recently by several papers that project coral responses to the climate change pathways in AR5 (RCPs 2.6, 4.5, 6.0, and 8.5). An analysis of the likely reef coral disease outbreaks resulting from ocean warming projected by RCP4.5 and RCP8.5 concluded that both pathways are likely to cause sharply increased, but spatially highly variable, levels of coral disease in the future, and that the outbreaks would be more widespread, frequent, and severe under RCP8.5 than RCP4.5 (Maynard et al. 2015). An analysis of the timing and extent of Annual Severe Bleaching (ASB) of the world's coral reefs under RCP4.5 vs RCP8.5 found that the global average timing of ASB would be only 11 years later under RCP4.5 than RCP8.5, and that >75% of all reefs still would experience ASB before 2070 under RCP4.5 (van Hooidonk et al. 2016).

An analysis of the responses of coral reefs to increased ocean warming and acidification under all four pathways in AR5 found that only RCP2.6 would allow the current downward trend in coral reefs to stabilize, and that RCP4.5 would likely drive the elimination of most coral reefs by 2040–2050 (Hoegh-Guldberg et al. 2017a), implying that RCP8.5 would be even worse. Hughes et al. (2017b) analyzed the responses of coral reefs to RCP2.6, and found that it would result in approximately the same amount of additional warming and bleaching by 2100 that has occurred over the last century, resulting in substantial additional degradation than has been observed so far (Hughes et al. 2017b). Another analysis regarding responses of coral reefs if global warming is limited to 1.5° C, 2.0° C, or 3° C from pre-industrial (i.e., roughly equivalent to: slightly less than RCP2.6, slightly more than RCP2.6, and approximately RCP4.5, respectively) found that estimated levels of thermal stress would be approximately seven, 11, and 23 times the level of thermal stress that these reefs have already experienced since 1878, and approximately two, three, and six times the level of thermal stress experienced in 2016 (Lough et al. 2018).

As the above summary shows, there is agreement in the coral reef literature that continuing on the path of RCP8.5 in the 21st century would have severe consequences for Indo-Pacific reef-building corals. The 4th US National Climate Assessment concurs, concluding that continued carbon emissions (i.e. RCP8.5) would transform coral reef ecosystems through the combined impacts of ocean warming and acidification later this century (USGCRP 2018). While the other pathways would not be as bad, even the low emissions pathways would still affect coral reef ecosystems because they represent continued warming over the present, such as RCP2.6 which would cause an additional, approximately 0.75° C of warming above the present (i.e., 1.75° C of warming above pre-industrial, see Fig. 1 above). The IPCC's 1.5° Report analyzed the impacts of an additional warming of 0.5° C on the world's reef-building corals (i.e., slightly less than RCP2.6, see Fig. 1 above), finding that even this amount of additional warming represents "very high risk of severe impacts," assuming that corals do not further acclimatize or adapt to the projected warming (Fig. 3-18, IPCC 2018).

Mean global ocean temperature changes in response to natural cycles, but the projected rate of ocean warming under RCP8.5 by 2100, would exceed natural rates of change by at least an order of magnitude, if not much more (Hoegh-Guldberg 2012). Although the acclimatization and adaptation capacities of reef-building corals provide some potential for colonies and populations to adjust to changing conditions, projected ocean warming is likely to exceed the capacities of many Indo-Pacific species over large portions of their ranges in the foreseeable future. Colonies of the Indo-Pacific reef-building coral *Acropora aspera* native to a highly-fluctuating environment (and thus thought to have high acclimatization capacity) failed to acclimatize to elevated seawater temperatures lower than those projected by RCP8.5 (Schoepf et

al. 2015). A study of *A. millepora* on the GBR demonstrated that its acclimatization capacity appears to be confined to the range of seawater temperatures historically experienced by a particular colony (Howells et al. 2013), yet projected temperatures would likely exceed these historical ranges in the foreseeable future. However, failure of individual colonies to acclimatize to changing conditions does not necessarily mean that the populations of which they are a part cannot adapt to the changing conditions. Another study of *A. millepora* on the GBR demonstrated that its adaptation capacity appears to be sufficient for it to adapt to warming of 0.1° C per decade over the next 100 years (Matz et al. 2018), but RCP8.5 would result in warming rates at least two or three times higher than this. Indeed, a study of the adaptive capacity of a population of *A. hyacinthus* in the Cook Islands concluded that it would go extinct under RCP8.5 by the year 2055 (Bay et al. 2017).

  <u>Ocean Warming Conclusion</u>. From the above analysis of ocean warming and its effects on Indo-Pacific reef-building corals, we conclude that: (1) substantial ocean warming, including in the tropical/subtropical Indo-Pacific, has already occurred and continues to occur; (2) ocean warming, including in the tropical/subtropical Indo-Pacific, is projected to continue at an accelerated rate in the future; (3) substantial warming-induced mass bleaching of Indo-Pacific reef coral communities has already occurred and continues to occur; (4) warming-induced mass bleaching of Indo-Pacific reef coral communities is projected to rapidly increase in frequency, intensity, and magnitude in the foreseeable future; and (5) Indo-Pacific coral reefs will be severely affected by such warming. Table 5 below shows when the onset of twice-per-decade and annual severe bleaching is projected to occur under RCPs 2.6, 4.5, and 8.5 at 25 Indo-Pacific and eastern Pacific coral reef locations. Under RCP8.5, the average year for the onset of twice-per-decade severe bleaching is 2032, and only ten years later for annual severe bleaching in 2042 (Heron et al. 2017). Based on the above information, we consider ocean warming to be the most important threat contributing to extinction risk of Indo-Pacific reef-building corals in the foreseeable future.

Table 5. <u>Example of Projected Coral Bleaching</u>: Onset of twice per decade and annual severe bleaching events at 25 UNESCO sites in the Indo-Pacific under RCPs 8.5, 4.5 and 2.6 (Caribbean site greyed out; reproduced with permission from Heron et al. 2017).

Reef-containing World Heritage site	Future Severe Stress - RCP8.5		Future Severe Stress - RCP4.5		Future Severe Stress - RCP2.6	
	(a) Projected Year of 2x/decade	(b) Projected Year of Annual	(c) Projected Year of 2x/decade	(d) Projected Year of Annual	(e) Projected Year of 2x/decade	(f) Projected Year of Annual
Great Barrier Reef	2035	2044	2041	2051	----	----
Lord Howe Island Group	2034	2043	2036	2055	----	----
Ningaloo Coast	2041	2049	2052	2074	----	----
Shark Bay, Western Australia	2038	2047	2045	2074	----	----
Belize Barrier Reef Reserve System	2028	2036	2036	2044	---	---
Brazilian Atlantic Islands	2025	2019	2035	2049	---	---
Malpelo Fauna and Flora Sanctuary	2038	2050	2056	2077	----	----
Cocos Island National Park	2019	2032	2028	2036	2062	----
Area de Conservación Guanacaste	2030	2043	2040	2055	----	----
Galápagos Islands	2017	2036	2027	2042	2070	----
Lagoons of New Caledonia	2031	2040	2039	2050	----	----
Komodo National Park	2017	2025	2021	2032	----	----
Ujung Kulon National Park	2032	2043	2042	2053	----	----
Ogasawara Islands	2030	2038	2041	2049	----	----
Phoenix Islands Protected Area	2020	2035	2028	2040	2038	----
Gulf of California	2044	2052	----	----	----	----
Archipiélago de Revillagigedo	2031	2042	2043	2052	----	----
Sian Ka'an	2025	2033	2033	2041	----	----
Rock Islands Southern Lagoon	2028	2036	2032	2044	----	----
Coiba National Park	2030	2043	2040	2053	2053	----
Tubbataha Reefs Natural Park	2030	2039	2037	2048	----	----
Aldabra Atoll	2028	2036	2034	2042	----	----
East Rennell	2025	2033	2030	2044	----	----
iSimangaliso Wetland Park	2031	2040	2036	2048	---	---
Sanganeb and Dungonab Bay-Mukkawar Island MNPs	2037	2046	2055	2069	----	----
Everglades National Park	2036	2044	2056	2071	---	---
Papahānaumokuākea	2029	2041	2044	2052	----	----
Ha Long Bay	2077	2086	----	----	----	----
Socotra Archipelago	2040	2048	2061	2077	----	----

Severe bleaching stress threshold defined as DHW of 8 °C-weeks.

	2025	2040	2055	never	onset

4.2.2.   Ocean Acidification (ESA Factor E)

Ocean acidification refers to the ongoing reduction in pH of the ocean from anthropogenic greenhouse gas emissions, and thus is considered under ESA Factor E – other natural or manmade factors affecting the continued existence of the species. Ocean acidification is caused by increased GHG accumulation in the atmosphere, and subsequent absorption by the oceans. Ocean acidification threatens reef-building corals by reducing coral skeletal calcification and reef cementation. In order to adequately describe this threat, we provide summaries of (1) observed ocean acidification to date; (2) projected ocean acidification in the foreseeable future (i.e., from now to 2100); (3) observed effects of ocean acidification on Indo-Pacific reef coral communities to date; and (4) projected effects of ocean acidification on Indo-Pacific reef coral communities in the foreseeable future.

<u>Observed Ocean Acidification</u>. The mean pH of the surface waters of the open ocean is currently approximately 8.1 pH units, ranging between 7.8 and 8.4 depending on location and season; as such, the ocean is mildly basic (pH > 7.0). Since the beginning of the industrial era in the mid-19th century, the release of CO_2 from industrial and agricultural activities has resulted in atmospheric CO_2 concentrations that have increased from approximately 280 ppm to over 410 ppm in 2019 (https://www.esrl.noaa.gov/gmd/ccgg/trends/, accessed December 2019). There has

been a corresponding increase in CO_2 uptake by the oceans, resulting in a reduction in the mean pH of surface waters of the open ocean of approximately 0.1 units from about 8.2 to 8.1 since the beginning of the industrial era (starting in the mid-19th century). Recent estimates of annual rates of pH reduction in the surface waters of the open ocean range from 0.0013 to 0.0024 units annually (IPCC 2013), corresponding to a rate of pH reduction of at least 0.1 units per century. This rate of pH change in the oceans exceeds any known in the last 300 million years (Honisch et al. 2012).

Ocean acidification reduces the aragonite saturation state (Ω_{arg}) in seawater by lowering the supersaturation of carbonate minerals including aragonite, which requires marine calcifiers like reef-building corals to expend more energy to calcify their skeletons (Langdon and Atkinson 2005), as described in more detail in the Calcification and Skeletal Plasticity section above. Generally, Ω_{arg} should be 3.5 or greater to enable maximum calcification of reef-building corals, and Ω_{arg} levels of <3 and 3.0-3.5 result in "extremely marginal" and "marginal" coral reef environments, respectively (Guinotte et al. 2003). Since the beginning of the industrial era, there has been an estimated mean decrease in Ω_{arg} of the surface waters of the open ocean in the tropical Pacific from about 4.5 to 3.8 (Feely et al. 2009, Feely et al. 2012), and a decrease of about 0.34 – 0.40% annually over the last two decades (Jiang et al. 2015). Many abiotic and biotic factors cause greater fluctuations and different mean values in pH and Ω_{arg} on coral reefs than in surface waters of the open ocean (Mongin et al. 2016, Shaw et al. 2012a), making changes in pH and Ω_{arg} on coral reefs difficult to distinguish from natural fluctuations, and more difficult to detect than changes in surface waters of the open ocean.

Despite the above challenges in detecting changes in pH and Ω_{arg} on coral reefs, several lines of evidence suggest that ocean acidification has been occurring on coral reefs for some time already, i.e., that pH and Ω_{arg} have already decreased in coral reef waters during the industrial era. For example, the Hawaii Ocean Time-series (HOT) and Bermuda Atlantic Time-series (BATS) oceanographic biogeochemical data collection projects both have been collecting pH and Ω_{arg} in tropical waters near coral reefs since the 1980s, and both show very similar results: (1) pH steadily decreased by 0.0016 (HOT) and 0.0017 (BATS) annually, and (2) Ω_{arg} steadily decreased by 0.0084 (HOT) and 0.0095 (BATS) annually. These rates correspond to pH reductions of 0.16 – 0.17 per century, and Ω_{arg} reductions of 0.84 – 0.95 per century (Bates et al. 2014). A comparison of pH and Ω_{arg} data and modeled pre-industrial pH and Ω_{arg} levels for two coral reef sites in the Pacific (Chuuk) and Caribbean (Puerto Rico) accounted for natural variability, and demonstrated that current pH and Ω_{arg} levels are significantly lower than pre-industrial levels at both sites (Sutton et al. 2016).

Projected Ocean Acidification. Under RCP8.5, mean pH of the surface waters of the open ocean in the tropics (20°N to 20°S) is projected to decline from the current pH of approximately 8.05 to approximately 7.95 by 2050, and to approximately 7.75 by 2100, or a reduction of 0.30 by 2100 (IPCC 2013, Fig. 6.28a). In the tropical Indo-Pacific, decreases of 0.25 to 0.40 are projected, with the lower reductions in the central and eastern Pacific, and the higher reductions in the GBR area and the northern Philippines (IPCC 2013, Fig. 6.28b). The pH reductions associated with RCP8.5 are projected to result in declining Ω_{arg} of the surface waters of the open ocean from current levels of over 3, to less than 2.5 by 2100 (IPCC 2013, Fig. 6.29f). We interpret the IPCC's projections of ocean acidification under RCP8.5 as follows: (1) mean pH of the surface waters of the open ocean in the tropics is projected to decline by approximately 0.31 to approximately 7.75 by 2100, with a subsequent large decline in Ω_{arg} in surface tropical waters; (2) pH and Ω_{arg} levels on Indo-Pacific coral reefs will also decline by roughly the same amount,

but spatial and temporal variability will be high; and (3) these changes will greatly exacerbate the impacts of ocean acidification on Indo-Pacific reef-building corals.

Observed Effects of Ocean Acidification. Ocean acidification affects reef-building corals in three main ways: (1) Decreased calcification rates of coral colonies, leading to lower skeletal growth rates; (2) increased dissolution of the calcium carbonate structure of coral reefs, leading to reef erosion rates outpacing accretion rates; and (3) effects on coral reproduction, leading to lower fertilization, settlement, and recruitment (Brainard et al. 2011). Observing such changes in the field and determining their cause is very difficult for many reasons including the interaction of different factors. For example, ocean acidification, ocean warming, and land-based sources of pollution may all interact to affect coral skeletal growth rates. However, there is currently some information available on the observed effects of ocean acidification on skeletal growth and reef dissolution in the Indo-Pacific, as described below.

As described in more detail the Calcification and Skeletal Growth section, calcification is the process by which reef coral colonies build their skeletons. Reduced calcification rates may result in slower skeletal growth, reduced skeletal density, and diversion of energy from other processes such as tissue growth or reproduction to maintain calcification. There is growing evidence that calcification and skeletal growth rates of some Indo-Pacific reef corals have decreased in recent decades, and that ocean acidification is likely a contributing factor. Several studies report decreasing skeletal growth rates in massive *Porites* colonies on the GBR (Cooper et al. 2009, De'ath et al. 2009, De'ath et al. 2013, Lough 2008) and in *Pocillopora* species in the eastern Pacific (Manzello 2010) over the last several decades. All five studies mentioned the interaction of ocean warming and acidification as a potential cause of the lower growth rates, but acknowledged that determining the true cause requires additional work. Reduced coral skeletal growth rates in the Red Sea since the 1990s was most likely due to ocean acidification (Steiner et al. 2018).

Coral reef structures are the accumulation of calcium carbonate ($CaCO_3$) from coral aragonite skeletons and other marine calcifiers such as crustose coralline algae. For reefs to exist, $CaCO_3$ accretion in the reef framework and sediments must be greater than $CaCO_3$ erosion via dissolution and physical loss. An analysis of 22 coral reef sites including 19 in the Indo-Pacific found that there have been major reductions in coral reef sediment precipitation and net ecosystem calcification during the industrial era because of the decreased Ω_{arg} levels that have already occurred (Eyre et al. 2018). In the Red Sea, the net contribution of reef corals to the $CaCO_3$ budget declined by approximately 100% between 1998 and 2015, and the most likely explanation is decreasing Ω_{arg} (Steiner et al. 2018). In the eastern Pacific, where Ω_{arg} levels are naturally low, increased reef erosion was observed after the bleaching events of the 1980s. Reef accretion was able to keep up with erosion before the bleaching events, but not afterwards, when erosion rapidly outpaced accretion. The low Ω_{arg} levels likely predisposed these reefs to high erosion rates when faced with additional stressors such as bleaching (Eakin 1996).

Projected Effects of Ocean Acidification. The effects of the lower Ω_{arg} projected for Indo-Pacific coral reef waters on coral calcification and growth, reef erosion, and coral reproduction have been extensively studied via laboratory experiments, modeling efforts, and at field sites with naturally low Ω_{arg} representative of projected conditions. Reviews of such studies summarize the projected effects on reef corals (Brainard et al. 2011) and marine calcifiers including reef corals and crustose coralline algae (Kroeker et al. 2013), as described below and supplemented by more recent studies. Projected effects on Indo-Pacific coral reef communities and ecosystems are also summarized.

A review of laboratory studies on the effects of ocean acidification on coral calcification projected for the foreseeable future on Indo-Pacific reef coral species found that all species responded with lower calcification rates, but that responses were highly species-specific. The review also included studies showing that skeletal growth rates of crustose coralline algae, one of the primary calcifiers on coral reefs, would be reduced by 86% (Brainard et al. 2011). A review of laboratory studies on the effects of ocean acidification "roughly representing year 2100 scenarios" on the survival, calcification, growth, photosynthesis, and abundance of several groups of marine calcifiers found that survival and calcification were affected the most, including 34% and 40% reductions in calcification of reef corals and mollusks, respectively. In addition, the study projected that reef corals and calcifying algae (including crustose coralline algae) would experience reductions in abundance of 47 and 80%, respectively (Kroeker et al. 2013). A review of laboratory studies on the effects of ocean acidification and ocean warming resulting from atmospheric CO_2 levels of >700 ppm (RCP8.5 = 936 ppm in 2100) on reef corals projected that calcification would be reduced by an average of 20% for all species, but with high species-specific variability (Kornder et al. 2018). A model of the effects of ocean acidification alone (i.e., without considering the additive effect of ocean warming) projected for the foreseeable future found that *Porites* skeletal density is likely to decrease by 20% (Mollica et al. 2018).

The ocean acidification projected for the foreseeable future is expected to result in erosion outpacing accretion on many Indo-Pacific reefs, just as it has already done on eastern Pacific reefs (Brainard et al. 2011). An analysis of 22 coral reef sites, including 19 in the Indo-Pacific, and the resulting model projected that 17 of the 19 sites would fall below Ω_{arg} levels of 2.92 by 2100, the threshold below which dissolution of reef sediments would exceed accumulation of reef sediments, thus demonstrating that reef erosion is outpacing reef accretion (Eyre et al. 2018). Field studies at Indo-Pacific sites with naturally acidic seawater show that reef erosion exceeds reef accretion at a pH of approximately 7.8 (Enoch et al. 2016), and that very high rates of reef erosion characterize such sites (Barkley et al. 2015). In addition to effects on coral calcification and reef erosion, the ocean acidification projected for the foreseeable future is also expected to lower the fertilization, settlement, and recruitment of some Indo-Pacific reef-building corals (Brainard et al. 2011).

Because of the above effects of projected ocean acidification on coral calcification, reef erosion, and coral reproduction, Indo-Pacific reef-building coral communities are expected to experience reductions in complexity and resilience, loss of reef corals, increases in macroalgae, simplification, and overall degradation. For example, within Indo-Pacific communities where naturally acidic seawater roughly approximates pH levels projected by 2100 (8.1 to 7.8), there is lower reef coral diversity, recruitment, and abundances than in other Indo-Pacific reef coral communities, suggesting that projected ocean acidification in the foreseeable future will reduce the complexity and resilience of these communities (Fabricius et al. 2011). Another study at a high latitude Indo-Pacific coral reef site with naturally acidic seawater showed that pH levels projected by 2100 are likely to result in the loss of reef corals, increase in macroalgae, and simplification of the community (Agostinin et al. 2018). A field experiment on an Indo-Pacific reef flat showed that the addition of CO_2 to simulate Ω_{arg} levels projected later this century resulted in a significant reduction in net calcification of the reef coral community, which would eventually simplify and degrade the community (Albright et al. 2018).

Ocean Acidification Conclusion. From the above analysis of ocean acidification and its effects on Indo-Pacific reef-building corals, we conclude that: (1) ocean acidification has already

occurred in the tropical/subtropical Indo-Pacific and continues to occur; (2) ocean acidification, including in the tropical/subtropical Indo-Pacific, is projected to continue at an accelerated rate in the future; (3) ocean acidification has already affected Indo-Pacific reef-building coral communities by reducing calcification rates and subsequent effects on skeletal growth (reduced growth rates and skeletal densities) of corals, and by increasing erosion of coral reefs; and (4) the effects of ocean acidification on Indo-Pacific reef-building coral communities are projected to steadily increase and broaden in the foreseeable future by reducing coral calcification, increasing reef erosion, impacting coral reproduction, reducing reef coral diversity, and simplifying coral reef communities.

4.2.3.   Sea-level Rise (ESA Factor E)

Sea-level rise refers to the ongoing increase in mean sea-levels around the world resulting from anthropogenic ocean warming, and thus is considered under ESA Factor E – other natural or manmade factors affecting the continued existence of the species. Rapid sea-level rise potentially threatens reef-building corals by requiring them to grow quickly to keep up with rising sea-levels, degrading water quality through increased coastal erosion, and compounding the effects of other simultaneous threats such as warming-induced bleaching and ocean acidification (Brainard et al. 2011). In order to adequately describe this threat, we provide summaries of the following: (1) Observed sea-level rise to date; (2) projected sea-level rise in the foreseeable future (i.e., from now to 2100); (3) observed effects of sea-level rise on Indo-Pacific reef coral communities to date; and (4) projected effects of sea-level rise on Indo-Pacific reef coral communities in the foreseeable future.

Observed Sea-level Rise. Ocean warming results in sea-level rise through ice melting and thermal expansion of seawater. Tide gauge observations show a global mean sea-level rise during the 20th century of approximately 1.7 mm per year, while satellite altimetry data indicate faster rates of between 2.8 and 3.6 mm per year since 1993. Total global mean sea-level rise during the industrial era is estimated at approximately 20 cm (IPCC 2013). Data also show that sea-level rise is not spatially uniform, with portions of the Indo-Pacific such as Tuvalu and Tokelau in the western tropical Pacific Ocean experiencing rates of sea-level rise approximately three times faster than the global mean since 1950 (Becker et al. 2012).

Projected Sea-level Rise. Sea-level rise is projected to accelerate in the foreseeable future due to the melting of land and sea ice and thermal expansion. Under RCP8.5, AR5 projects that global mean sea-level will rise approximately 740 mm by 2100 relative to sea-level during the period from 1986 to 2005 (IPCC 2013, Table 13.5). More recent research suggests ice melting rates are likely to increase more rapidly than projected by RCP8.5, further accelerating sea-level rise (Bronselaer et al. 2018, Trusel et al. 2018). It is important to note that projected regional sea-level rise differs substantially from the projected global mean for some Indo-Pacific coral reef areas: The Red Sea, Persian Gulf, and nearshore areas of the northern Indian Ocean are projected to rise less than the projected global mean, whereas portions of the western and central Pacific are projected to rise at or slightly more than the projected global mean (IPCC, Figure 13.20d).

Observed Effects of Sea-level Rise. There is little information available on the effects of sea-level rise during the industrial era (since the mid-19th century) on Indo-Pacific corals, most likely because the sea-level rise in much of the region so far has been slow and small, making detection of any biological response difficult. However, sea-level has risen approximately 5 cm per year (≈3x the global mean) at Funafuti Atoll in Tuvalu over the past 60 years, providing a natural laboratory for studying the effects of sea-level rise on coral atolls. A study on the impacts of sea-level rise on Funafuti did not detect increased erosion, and in fact found that the

aggregated land area of the islands of Funafuti Atoll increased by 7.3% over the past century despite the sea-level rise. The study did not investigate the response of the reef-building coral community to the sea-level rise (Kench et al. 2015). In the Solomon Islands in 2007, an earthquake caused 300-700 mm subsidence of coral reef areas, equating to that amount of instantaneous sea-level rise for the coral reefs there. Reef-building corals responded with a 157% increase in coral cover over seven years, because fast-growing *Acropora* species colonized newly-available substrates (Albert et al. 2017). However, an analysis of >100 Indian Ocean coral reefs found that mean post-bleaching reef vertical accretion rates (i.e., the amount of upward growth of the reef in mm/yr) were less than recent sea-level rise rates for nearly half of the reefs studies, implying that frequently-bleached reefs may already be unable to keep up with current sea-level rise (Perry et al. 2018). Collectively, studies to date indicate that the effects of sea-level rise on Indo-Pacific reef-building corals are complex, with no clear trend yet apparent.

Projected Effects of Sea-level Rise. Under RCP8.5, mean global sea-level rise of 11.2 mm per year is projected to occur by 2081-2100 (IPCC 2013, Table 13.5), in comparison to approximately 1.7 mm per year of sea-level rise that occurred during the 20th century. An analysis of >100 Indian Ocean coral reefs found that mean post-bleaching reef accretion rates were less than projected sea-level rise rates under RCP8.5 for nearly all of the reefs studied, emphasizing how the impacts of bleaching on coral growth undermines their capacity to keep up with projected sea-level rise (Perry et al. 2018). The mean current carbonate production rate at 24 sites on Palau and Yap are estimated to result in a potential future mean accretion rate of 7.9 mm per year (van Woesik and Cacciapaglia 2018). These vertical accretion rates approach those projected under RCP8.5. However, the historical capacity of these corals to keep up with rising sea-levels is now compounded by the increased erosion that would occur from human-altered coastlines and watersheds, and the interaction of other simultaneous threats such as warming-induced bleaching and ocean acidification. Fringing reefs will be susceptible to increasing erosion and subsequent sedimentation caused by increasing rates of sea-level rise, due to their proximity to shorelines and watersheds heavily impacted by human activities (Field et al. 2012). This is especially true for the reef flats component of fringing reefs, as they lie between the coastline and the reef crest, which will be most exposed to the increased erosion and sedimentation (Ogston and Field 2010).

Sea-level Rise Conclusion: From the above analysis of sea-level rise and its effects on Indo-Pacific reef-building corals, we make the following conclusions: (1) Sea-level rise has already occurred and continues to occur globally; (2) sea-level rise in parts of the tropical/subtropical Indo-Pacific has been approximately three times the global rate; (3) sea-level rise projected under RCP8.5 will far exceed recent sea-level rise rates both globally and in the Indo-Pacific; (4) the effects of sea-level rise to date on Indo-Pacific reef-building corals are complex, with no clear trend yet apparent; and (5) the effects of sea-level rise on Indo-Pacific reef coral communities are projected to steadily increase and broaden in the foreseeable future RCP8.5. These effects include potential reef submergence if reef accretion cannot keep up, degradation of water quality in nearshore habitats such as reef flats by increased coastal erosion, and compounding the effects of other simultaneous threats such as warming-induced bleaching and ocean acidification.

4.2.4.   Fishing (ESA Factor A)

Fishing here refers to the harvest of finfish, mollusks, crustaceans, and other forms of marine animal and plant life on or in the vicinity of shallow coral reefs and reef-building corals, either for food or for the aquarium trade. Harvest of corals themselves is treated separately under

Collection and Trade below. Fishing affects the habitat of Indo-Pacific reef-building corals, and thus is considered under ESA Factor A – the present or threatened destruction, modification, or curtailment of its habitat or range. Fishing directly affects reef-building coral habitat by destroying and modifying benthic substrates, and indirectly by altering trophic interactions that are important in structuring coral reef ecosystems. In order to adequately describe this threat, we provide summaries of (1) Observed effects of fishing on Indo-Pacific reef-building corals to date; and (2) projected effects of fishing on Indo-Pacific reef-building corals in the foreseeable future (i.e., from now to 2100).

Observed Effects of Fishing. The ranges of Indo-Pacific reef-building corals overlap with some of the densest human populations in the world (e.g., Indonesia, Philippines, Vietnam, India, etc.). Hundreds of millions of people live near Indo-Pacific coral reefs, many of whom depend on coral reef fisheries for food and income, thus fishing on coral reefs is particularly intense in many of these areas. An assessment of the risks to the coral reefs of the world found that >90% of the coral reefs in Southeast Asia are at medium or high risk from fishing. Human population has rapidly grown in these areas, at the same time that technology (fishing gear and boats) has improved and become more economical, resulting in rapid growth in fishing around coral reefs in recent decades. Most coral reef fisheries are small-scale fisheries, and thus are poorly represented in global fisheries statistics. However, where national figures are available, such as for Indonesia and the Philippines, they indicate not only that the growth in coral reef fisheries is unsustainable for the coral reef fish stocks, but that coral reef habitats are being damaged and destroyed by fishing at an unprecedented rate. Unsustainable fishing of some species is reported even on some of the most remote and best-protected coral reefs in Southeast Asia (Burke et al. 2011).

Fishing directly affects the habitats of reef-building corals and the coral colonies themselves when various gears or fishing methods interact with reef substrates. Common methods include various types of nets and traps, hook-and-line, and spearfishing. Both active and derelict fishing gear can destroy benthic structure and habitats, kill reef-building organisms, and entangle benthic and mobile fauna. As an example of the amount of derelict fishing gear affecting coral reefs, at least 52 metric tons of derelict fishing gear drift from distant fisheries (thousands of kilometers away) and become entangled on reefs of the remote Northwestern Hawaiian Islands annually. Trawl nets dislodge and abrade corals, while stationary gear such as traps damage corals and other sessile fauna via movement during even mild storm events and during gear retrieval in adverse conditions. Storms can mobilize traps and cause buoy lines to snare branching corals (Brainard et al. 2011).

Fishers in some parts of the world employ explosives or poison to harvest fish and invertebrates. These practices have been concentrated on coral reefs in Southeast Asia, the western Pacific, and eastern Africa. Most notable is the use of explosives to kill or stun fish, which destroys coral in the process. Although illegal in many countries, blast (or dynamite) fishing has been widely used in some locations. Poison fishing typically involves using cyanide to stun and capture fish live. The poison can bleach corals and kill polyps. Fishers often break corals to extract the stunned fish, while other species in the vicinity are killed or left vulnerable to predation (Burke et al. 2011).

Most of the fishing described above targets food fish for local markets. The collection of reef fish for the global marine aquarium trade is another type of direct impact of coral reef fishing. Globally, millions of live coral reef fish are collected from dozens of Indo-Pacific countries each year using various gears and methods such as nets, traps, and poisons that damage

or destroy reef-building coral habitats and the corals themselves. Collection of some coral reef fish for the marine aquarium trade has caused virtual extirpation of local populations, major changes in age structure, and promotion of collection practices that destroy reef habitats (Brainard et al. 2011). The collection of reef-building corals for the marine aquarium trade is covered separately below under Collection and Trade.

In addition to the direct effects of fishing described above, fishing can also have indirect effects such as increasing algal growth on coral reefs due to reducing population abundance, species richness and size of herbivorous fish, and increasing predation on corals by releasing corallivores from predator control. These types of indirect effects are collectively referred to as trophic effects of fishing because of their impacts on food web dynamics, AKA trophic interactions. Thus, an important aspect of maintaining resilience in coral reef ecosystems is to sustain populations of herbivores, especially the larger species such as parrotfish. On topographically complex reefs, population densities can average well over a million herbivorous fishes per km^2, and standing stocks can reach 45 metric tons per km^2. Under conditions of topographic complexity with substantial populations of herbivorous fishes, as long as the cover of living coral is high and resistant to mortality from environmental changes, it is very unlikely that algae will take over and dominate the substrate. However, if herbivorous fish populations, particularly large-bodied parrotfish, are fished down, then algae can grow rapidly in the absence of herbivorous fish, thus preventing the recovery of the coral population. These effects are exacerbated when a major mortality of coral colonies occurs (e.g., via a bleaching event), because the algae has more substrate to grow on (Brainard et al. 2011). Such trophic effects have been widely documented in Caribbean coral reef ecosystems where heavily fished herbivorous fish populations typically cannot maintain high rates of herbivory on algae (Jackson et al. 2014). In the Indo-Pacific, so far there have been fewer observed cases of such trophic effects of fishing on coral habitat because: (1) In those areas that are best studied (e.g., Hawaii), fisheries are generally focused on piscivorous fish species rather than herbivorous fish species (Friedlander and DeMartini 2002), thus herbivorous fish populations are less fished down in more of the Indo-Pacific than in the Caribbean; and (2) Indo-Pacific herbivorous reef fish assemblages are more diverse than in the Caribbean, making them relatively resilient in the sense that Indo-Pacific reef fish communities have a higher capacity to be fished while maintaining high rates of herbivory (Edwards et al. 2014).

Projected Effects of Fishing. As noted above, the ranges of Indo-Pacific reef-building corals overlap with human populations that are already some of the densest in the world. The projected effects of fishing on Indo-Pacific reef-building corals from now to 2100 are directly linked to human population, which is projected to grow from current global numbers of 7.7 billion to between 9 and 11 billion. Furthermore, the human population near coral reefs in much of the Indo-Pacific, especially in Southeast Asia, is expected to grow at a higher rate than the mean global human population (World Bank 2011), which is supported by recent population growth statistics. The six countries of the Coral Triangle (Malaysia, Indonesia, Australia, Philippines, Papua New Guinea, Solomon Islands) have over half of the coral reef area in the Indo-Pacific (Spalding 2001) and most of the reef-building coral biodiversity (Veron et al. 2015); yet these six countries had a mean annual human population growth rate of 1.41% in 2017, compared to the global human population growth rate of 1.06% in 2017 (World Fact Book, 2017). An additional factor that is likely to result in increasing impacts of coral reef fishing in the foreseeable future is the likely advancement of fishing technologies (fishing gear, boats, etc.),

which will further increase the capacity of the fisheries to find and catch fish even from distant and deep coral reefs (Brainard et al. 2011).

Although some parts of the Indo-Pacific are experiencing decreasing populations as people migrate to urban areas within their countries or to other countries (for example, Indo-Pacific island countries with negative population growth in 2017 included the Cook Islands (-2.79%), Federated States of Micronesia (-0.52%), the Maldives (-0.06%), and Tonga (-0.05%)), over 90% of Indo-Pacific coral reef countries, including those with the most coral reef area, had positive human growth rates in 2017 (World Fact Book, 2017). Thus, it is likely that the direct effects of fishing will increase throughout most of the Indo-Pacific in the foreseeable future, simply because there will be more people and more demand for fish, hence more fishing activity. Likewise, while indirect effects have so far not been observed to be as pronounced in the Indo-Pacific as in the Caribbean, the projected increases in human populations and fishing pressure described above in the Indo-Pacific are likely to eventually cause an increase in indirect effects.

Fishing Conclusion. From the above analysis of direct and indirect effects of fishing on Indo-Pacific reef-building corals, we conclude that: (1) Direct effects of fishing, namely damage from fishing gears and methods used in food fish and marine aquarium fisheries, have been observed in much of the Indo-Pacific; (2) indirect effects, or the trophic effects of fishing, have not been observed in the Indo-Pacific as they have in the Caribbean; and (3) both direct and indirect effects of fishing are projected to increase in the Indo-Pacific in the foreseeable future.

4.2.5. Land-based Sources of Pollution (ESA Factor A)

Land-based sources of pollution refer to sediment, nutrients, contaminants, and other types of pollution affecting reef-building corals that originate from coastal development, urbanization, agriculture, and other human activities on land, and thus are considered under ESA Factor A – the present or threatened destruction, modification, or curtailment of its habitat or range. The many different forms of land-based sources of pollution collectively affect all life history stages of reef-building corals in numerous ways. In order to adequately describe this threat, we provide summaries of (1) observed effects of land-based sources of pollution on Indo-Pacific reef-building corals to date; and (2) projected effects of land-based sources of pollution on Indo-Pacific reef-building corals in the foreseeable future (i.e., from now to 2100).

Observed Effects of Land-based Sources of Pollution. In the 1990s, it was estimated that approximately half of the world's coral reefs were threatened by land-based sources of pollution (Bryant et al. 1998). A more recent assessment concluded that coastal human populations and subsequent coastal development continued to increase land-based sources of pollution and impacts to coral reefs (Burke et al., 2011). Human activities in coastal watersheds introduce sediment, nutrients, contaminants, and other pollutants into the ocean by various mechanisms, including river discharge, surface runoff, groundwater seeps, and atmospheric deposition (Brainard et al. 2011). Sediment and turbidity, nutrients, and contaminants are each discussed separately below.

Sediment and Turbidity: Human activities in coastal and inland watersheds introduce terrestrial sediment into the ocean by river discharge and surface runoff. Elevated terrestrial sediment levels are generated by poor land use practices and coastal and nearshore construction. Terrestrial sediments tend to be both finer (more easily re-suspended) and darker (more light-absorbing) than marine sediments, thus reducing light more effectively when suspended in the water column. The high iron content of some terrestrial sediments may also serve as fertilizers to certain components of some coral reef systems. Further, terrestrial sediments are often associated with harmful organic compounds, heavy metals, nutrients, or harmful bacteria. Effects on corals

depend on grain size and organic content of the sediment, as well as the amount of sediment and the duration of the sediment stress (Brainard et al. 2011).

The fact that agriculture, mining, and logging can sharply increase sedimentation of coral reefs has been observed in the Indo-Pacific for many decades (Risk and Edinger 2011). A study of sedimentation on the GBR between 1750 and 1998 found that sediment from river floods reached the inner GBR occasionally until about 1870 when European settlement began, then increased by five to 10-fold due to land-use practices such as land clearing for agriculture and livestock grazing (McCulloch et al. 2003). Similarly, a study of sedimentation on a Hawaiian reef found that sediment from streams greatly increased on the reef in the early 1900s after a rapid increase in land clearing for the same reasons (Prouty et al. 2010). Elsewhere in the Indo-Pacific, some of the most rapid logging and land clearing in the world occurred in the Coral Triangle and east Africa in the early 21st century (Burke et al. 2011). Exposure to sedimentation can be moderated by distance of some coral habitats from areas where sedimentation is chronically or sporadically heavy, resulting in some habitats being less affected by sedimentation. Exposure to sedimentation for particular species may also be moderated by depth of habitats (Brainard et al. 2011).

As described above in Habitat Requirements, the settlement and recruitment of reef-building corals require consolidated hard substrate that is sediment-free. Sediment accumulation has been observed to result in a variety of lethal and sub-lethal effects of all life stages of Indo-Pacific reef-building corals (i.e., adults, fragments, larvae, and recruits). Sediment may prevent settlement of larvae in the first place. Once a coral is settled and has started to grow into a colony, the most common direct effect of sediment is deposition on the colony's surfaces. Corals with certain morphologies (e.g., mounding) can passively reject settling sediments. In addition, corals can actively displace sediment by ciliary action or mucous production, both of which require energetic expenditures. Corals with large corallites tend to be better at actively rejecting sediment. Corals that are unsuccessful in removing sediment will be smothered and may eventually die, although a few species can tolerate complete burial for short periods of time. Sediment can also induce sublethal effects, such as reductions in tissue thickness, polyp swelling, zooxanthellae loss, and excess mucus production. Sedimentation also impedes fertilization of spawned gametes and reduces larval settlement and survival of recruits and juveniles (Fabricius et al. 2005, Erftemeijer et al. 2012, Browne et al. 2015, Rogers 1990).

Reduced water clarity, or turbidity, results from particles of sediment, organic matter, or plankton in the water, and so is often associated with elevated sedimentation and nutrients. Reef-building corals naturally occur across a broad range of water clarity levels from very turbid waters on enclosed reefs near river mouths to very clear waters on offshore barrier reefs, and many intermediate habitats such as open coastal and mid-shelf reefs (Browne et al. 2012). Turbidity is caused by suspended abiotic and biotic particulate matter (esp. clay and silt-sized particles) and some dissolved substances, which reduce light penetration. Fine clays and organic particles are easily suspended from the sea floor, reducing light for prolonged periods while undergoing cycles of deposition and re-suspension. Suspended fine particles also carry nutrients and other contaminants. Increasing turbidity results in less light available for zooxanthellae, thereby reducing photosynthesis which in turn reduces coral skeletal growth. As levels of sediment, turbidity, and nutrients increase over time in response to land-based sources of pollution, the coral community composition may shift from coral-dominated to macroalgae-dominated (De'ath and Fabricius 2010, Fabricius 2005, Fabricius et al. 2014).

Nutrients. Reef-building corals are able to live in nutrient-poor oceanic waters because of efficient nutrient recycling between the host coral and its symbiotic zooxanthellae. This makes the availability of nutrients highly influential in the function and status of corals and coral reef ecosystems, as too few nutrients are limiting but too many nutrients can result in detrimental ecological imbalances. As described above in Habitat Requirements, reef-building corals require suitable nutrient levels necessary for the successful completion of all life history stages. As with all plants, zooxanthellae require dissolved inorganic nutrients (nitrates and phosphates) for photosynthesis. Major natural sources of nutrients to coral reefs include upwelled deep water, groundwater seeps, and terrestrial runoff. Natural mechanisms for delivering nutrients to coral reefs are sometimes enriched by human activities, such as agriculture, forestry, and urbanization which produce nutrients (e.g., in fertilizers, wastewater, etc.) that make their way to corals reefs via point and non-point sources such as river discharges, groundwater, and municipal outfalls. Such anthropogenic nutrient sources may also bring other stressors, such as sediments and contaminants (Brainard et al. 2011, Burke et al. 2011).

Elevated nutrients have been observed to affect Indo-Pacific reef-building corals through at least three mechanisms: (1) Direct impacts on coral physiology; (2) indirect effects through nutrient-stimulation of other community components (e.g., macroalgae seaweeds, turf/filamentous algae, cyanobacteria, and filter feeders) that compete with corals for space on the reef; and (3) other indirect effects such as stimulation of plankton growth that increases turbidity, thereby reducing light availability for corals. Increased nutrient levels generally lead to higher zooxanthellae density, but lower energy transferred to the coral host, making the coral more susceptible to stressors such as elevated seawater temperatures. Other direct effects include decreased calcification and skeletal density. Excessive nutrient levels are generally detrimental to coral reproduction by inhibiting gamete development, reducing fertilization success, and reducing larval settlement (Fabricius 2005, Ferrier-Pages et al. 2000, Harrison and Ward 2001).

The most important indirect effect of excessive nutrients is stimulation of non-coral organisms and subsequent alteration of the competitive balance on the reef. One of the best known examples of the indirect effects of excessive nutrients levels is provided by Kaneohe Bay, Hawaii, where 25 years of municipal sewage effluent being discharged into the bay led to massive outbreaks algae and reductions in coral cover of >50% until the discharges ceased in the late 1970s (Hunter and Evans 1995). Most commonly, excessive nutrients lead to increased growth of turf algae and macroalgae, and the widespread increase in such algae on coral reefs in many populated areas has often been attributed to nutrient enrichment. However, experimental nutrient addition in some reef systems has not resulted in algal overgrowth because of the control of macroalgal standing stock by herbivores (Brainard et al. 2011). A meta-analysis comparing nutrient and herbivory effects indicated that herbivores generally have stronger control of algal abundance on tropical reefs than nutrient enrichment, and nutrient effects are often detectable only under conditions of reduced herbivory (Burkepile and Hay 2006).

Nutrient enrichment can also stimulate the production of particulate matter such as plankton, leading to an increase in filter feeders such as sponges and zoanthids. Many filter feeders are destructive bioeroders, thus nutrient enrichment and subsequent increases in bioeroders can shift reefs from net accretion to net erosion. Generally, excessive nutrients and associated stresses on coral populations lead to reduction in coral cover, shifts in coral community composition, and under at least some conditions (e.g., reduced herbivory and/or restricted circulation), increased algal biomass (Brainard et al. 2011).

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Contaminants. As with sediment and nutrients, contaminants may be delivered to coral reefs via either point or non-point sources on land, but also may originate from marine-based sources. Land-based sources of contaminants typically enter the ocean via rivers, groundwater, and direct runoff. The major groups of land-based contaminants that affect reef-building corals are heavy metals, hydrocarbons, pesticides, and personal care products. The effects of these four groups of contaminants on reef-building corals in the field, or in laboratory experiments using conditions that replicate polluted waters, are summarized here.

Heavy metals (e.g., Cu, Cd, Mn, Ni, Co, Pb, Zn, Fe) can be beneficial to coral health and growth when they occur at naturally low levels; however, at increased concentrations, they can be toxic. Heavy metals are persistent in the environment and can bioaccumulate. They are adsorbed into sediment particles, which can result in their long-distance transport away from sources of pollution. Corals incorporate metals in their skeleton and accumulate them in their soft tissue. Although heavy metals can occur in the marine environment from natural processes, in nearshore waters they are mostly a result of anthropogenic sources, whether land-based (e.g., wastewater, land-filling, industrial discharge, and agricultural activities) or marine-based (antifouling and anticorrosive paints from marine vessels and structures, shipping and other maritime activities, harbor and channel dredging, etc.), and are thus concentrated near cities, ports, and industrial developments. The effects of copper on corals include physiological impairment, impaired photosynthesis, bleaching, reduced growth, and DNA damage. Effects to fertilization, larval development, larval swimming behavior, metamorphosis, and larval survival have also been documented. Toxicity of copper was found to be higher when seawater temperatures are elevated. Nickel and cobalt can also have negative effects on corals, such as reduced growth and photosynthetic rates, and reduced fertilization success. Chronic exposure of corals to higher levels of iron may significantly reduce growth rates (Brainard et al. 2011, SERO 2016).

Hydrocarbons are found in fossil fuels such as oil and coal and can be produced by the incomplete combustion of organic matter. Hydrocarbons disperse through land-based non-point sources such as road run-off, sewage, and deposition of particulate air pollution. Hydrocarbons can also disperse from marine-based point sources such as oil spills and industrial sites. Studies have found effects of oil pollution on corals include growth impairments, mucus production, and decreased reproduction, especially at increased temperature (SERO 2016). Hydrocarbons have also been found to affect early life stages of corals. For example, natural gas exposure resulted in abortion of *Pocillopora damicornis* larvae during early embryogenesis and early release of larvae during late embryogenesis, with higher concentrations of natural gas yielding higher adverse effects (Villanueva et al. 2011). Hydrocarbon concentrations similar to those after an oil spill inhibited metamorphosis of *Acropora tenuis* larvae and sensitivity increased when co-exposed to "shallow reef" UV light levels (Negri et al. 2016).

Pesticides can also originate from land-based sources like agriculture or marine-based sources like harbors. They include herbicides, insecticides, and antifoulants used on vessels and other marine structures. Pesticides can affect non-target marine organisms like corals and their zooxanthellae. Corals have been shown to bioaccumulate pesticides such as lindane, heptachlor, chlordane, and dichlorodiphenyltrichloroethane (DDT). Adult corals are usually not directly affected by herbicides, but zooxanthellae have been shown to be affected at very low concentrations (Brainard et al. 2011). Diuron, an herbicide found in floodwaters on the GBR, is highly toxic to corals (Shaw et al. 2012b). Irgarol, an additive in copper-based antifouling paints, reduces settlement (Knutson et al. 2012) and inhibits photosynthesis (Jones and Kerswell 2003).

Additionally, pesticides can significantly inhibit coral reproductive processes, inhibiting fertilization, settlement, or metamorphosis (Markey et al. 2007).

Personal care products contain compounds that can act as contaminants when they enter the marine environment. Benzophenone-2 (BP-2) is a chemical additive to personal care products (e.g., shampoo, body lotions, soap, and detergents), product coatings (oil-based paints, polyurethanes), acrylic adhesives, and plastics that protects against damage from ultraviolet light. BP-2 is a known endocrine disruptor and a DNA mutagen. Benzophenone-3 (BP-3; oxybenzone) is an ingredient in sunscreen and personal care products (e.g., hair cleaning and styling products, cosmetics, insect repellent, soaps) that protects against damage from ultraviolet light. Oxybenzone can cause DNA mutations and is a skeletal endocrine disruptor. BP-2 and BP-3 have been shown to deform the larvae of *Stylophora pistillata* (Downs et al. 2014, Downs et al. 2016). Surfactants are used as detergents and soaps, wetting agents, emulsifiers, foaming agents, and dispersants. Linear alkylbenzene sulfonate (LAS) is one of the most common surfactants in use. Exposure of *Pocillopora verrucosa* to LAS has been shown to result in tissue loss (Kegler et al. 2015). These chemicals are released into the ocean through municipal wastewater discharges, landfill leachates, residential septic fields and unmanaged cesspits, as well as swimmers wearing products containing these chemicals.

Projected Effects of Land-based Sources of Pollution. As noted above in the Fishing section, the human population near coral reefs in much of the Indo-Pacific, especially in the Coral Triangle where more than half of all Indo-Pacific coral reefs are located and where most coral biodiversity is concentrated, is expected to grow at a higher rate than the mean global human population in the foreseeable future, as it has in recent decades. Thus, it is likely that the effects of land-based sources of sediment, nutrients, and contaminants will increase throughout most of the Indo-Pacific, simply because there will be more people and more human activities that generate each type of pollution. In addition, nearshore sediment levels and subsequent turbidity will also likely increase with sea-level rise. Greater inundation of reef flats can erode soil at the shoreline and re-suspend lagoon deposits, producing greater sediment transport and potentially leading to leeward reefs being flooded with turbid lagoon waters or buried by off-bank sediment transport.

Land-based Sources of Pollution Conclusion. From the above analysis of the effects of land-based sources of sediment, nutrients, and contaminants on Indo-Pacific reef-building corals, we conclude that: (1) effects of all three types of pollution have been observed in much of the Indo-Pacific, namely impacts on coral growth, reproduction, and survival in areas with the highest levels of pollution; and (2) such effects are projected to increase in much of the Indo-Pacific in the foreseeable future.

4.2.6.   Coral Disease (ESA Factor C)

Coral disease refers to infectious diseases of reef-building corals (not to coral bleaching or toxicological effects, which are covered elsewhere), and thus is considered under ESA Factor C – disease or predation. Coral diseases adversely affect various coral life history stages by causing adult mortality, reducing reproductive success, and impairing colony growth. In order to adequately describe this threat, we provide summaries of (1) observed coral diseases in the Indo-Pacific to date; and (2) projected coral diseases in the Indo-Pacific in the foreseeable future (i.e., from now to 2100).

Observed Coral Diseases. Although not as severe as in the Caribbean, coral diseases are a threat to Indo-Pacific reef-building corals. Coral diseases are a natural phenomenon on Indo-Pacific coral reefs, first being recorded in the early to mid-1800s (Roff 2016). Region-wide

patterns of prevalence of coral diseases (i.e., proportion of colonies with disease) in the Indo-Pacific are difficult to determine because of the high diversity of both reef-building coral species and their diseases, the vast size of the region, and the lack of data across the appropriate spatial and temporal scales. Some of the most common coral diseases are white syndrome (WS), black band disease (BBD), brown band disease, and skeletal eroding band, but the most common diseases vary by location, season, habitat, and other factors (Myers and Raymundo 2009).

As part of a worldwide study of coral diseases conducted in 2004 to 2006, surveys were conducted at 241 sites on the GBR, in the Northwestern Hawaiian Islands (NWHI), and in the Philippines. Total mean annual coral disease prevalence rates were 4.6% of colonies in the Philippines, 1.3% of colonies on the GBR, and 0.02% of colonies in NWHI. WS and BBD were the most common diseases in the Indo-Pacific (Ruiz-Moreno et al. 2012). The NOAA Coral Reef Ecosystem Program monitors the coral reefs of the U.S. Pacific Islands and includes coral diseases in its surveys. Monitoring surveys conducted from 2002 to 2006 in the American Samoa archipelago reported total coral disease prevalence rates per island ranging from 0.04% on Swains Island to 0.5% on Tutuila (Brainard et al. 2008). Monitoring surveys conducted from 2003 to 2007 in the Mariana Islands reported total coral disease prevalence rates per island ranging from 0.1% on Rota Island to 1.4% on Guam (Brainard et al. 2012). These studies give us a general idea of coral disease prevalence rates across the region, but do not provide trend information that might indicate temporal patterns.

The Australia Institute of Marine Sciences (AIMS) has been monitoring coral diseases on the GBR since the mid-1990s. Between 1999 and 2003, coral diseases increased rapidly on the GBR, and an analysis of the AIMS data from that time showed a 20-fold increase in WS (Willis et al. 2004), which correlated with the 1998 and 2002 warming-induced bleaching events. The 2008 GBR Status Report stated that after a peak in 2003, coral diseases declined in most GBR sub-regions but then returned to intermediate levels in 2006 and 2007 (AIMS 2008). The AIMS monitoring data collected on the GBR since 1999 do not show clear temporal trends in coral diseases, however there are indications that the GBR's reefs are increasingly stressed by multiple and increasing threats, thus the likelihood of coral diseases is thought to be increasing (AIMS 2014, AIMS 2017).

Coral diseases in the Indo-Pacific may have increased over the last few decades, but evidence is more anecdotal than quantitative. An analysis of trends in marine diseases over the last several decades found that coral disease has increased globally, but the increase was driven by trends in the Caribbean (Tracey et al. 2019). What is indisputable is that other threats to reef-building corals have rapidly increased during this period in the Indo-Pacific, as described above for Ocean Warming and other threats. Coral diseases are a complex response to various environmental stressors (Ban et al. 2013), many of which are being driven up by these threats, which often act synergistically with each other (Ateweberhan et al. 2013, Brainard et al. 2011). While it is unclear whether coral diseases have increased in the Indo-Pacific over the last few decades, the environmental stressors make coral more susceptible to diseases have increased.

Projected Coral Diseases. Maynard et al. (2015) projected how future climate conditions will increase coral susceptibility to disease, pathogen abundance, and pathogen virulence globally under RCP8.5. They concluded that RCP8.5 is likely to cause sharply increased, but spatially highly variable, levels of coral diseases between now and 2100 in the Indo-Pacific, and that coral diseases are as likely to cause coral mortality as bleaching in the coming decades (Maynard et al. 2015). However, the model used by Maynard et al. (2015) was criticized as being unrealistic, and not supporting the conclusion of such widespread coral mortality from diseases

in the future (Lesser and van Woesik 2015). A model of projected white plague disease in Red Sea reef corals over the next 80 years found that epidemics are increasingly likely, but that the patchy distributions and densities of coral colonies will limit transmission and restrict local epidemics (Zvuloni et al. 2015).

Coral Disease Conclusion. From the above analysis of coral diseases and their effects on Indo-Pacific reef-building corals, we conclude that (1) coral diseases and subsequent mortalities of Indo-Pacific reef-building corals are being increasingly observed, and while quantifiable temporal trends are lacking, the environmental stressors that lead to coral diseases (especially ocean warming) have clearly increased; and (2) environmental stressors that lead to coral diseases are projected to increase sharply in the Indo-Pacific in the foreseeable future under RCP8.5, thus coral diseases and subsequent coral mortalities are also likely to increase.

4.2.7. Predation (ESA Factor C)

Predation refers to feeding upon reef-building corals by corallivorous species of fish and invertebrates (e.g., snails and seastars), and thus is considered under ESA Factor C – disease or predation. Although predation is a natural process, it is considered an important threat to Indo-Pacific reef-building corals because of the observed and projected increases in human disturbances which allow predation to affect corals more than it otherwise would (Brainard et al. 2011). In order to adequately describe this threat, we provide summaries of (1) observed effects of predation on Indo-Pacific reef-building corals to date, and (2) projected effects of predation on Indo-Pacific reef-building corals.

Observed Effects of Predation. In undisturbed conditions, the distribution of corals is affected by predation by fishes and invertebrates. However, if the living coral cover is substantially reduced by natural or anthropogenic disturbances, the effects of predation become more substantive even if the rate of predation does not change. Over-predation can lead to significant coral declines when the rate of coral predation relative to the rate of healing or population replenishment of the prey crosses a threshold beyond which predation prevents the recovery of coral populations (Brainard et al. 2011).

Predation on some Indo-Pacific reef-building coral genera, especially *Acropora, Montipora, Pocillopora*, and *Porites*, by many corallivorous species of fish and invertebrates (e.g., crown-of-thorns seastar (COTS) and snails) is a chronic, though occasionally acute, energy drain and threat to corals (Cole et al. 2008), and has been identified for most coral life stages. The distribution of corals can be directly limited by predation of corallivorous fishes and invertebrates (Brainard et al. 2011). COTS outbreaks are among the most significant biological disturbances that occur on Indo-Pacific coral reefs, since they can wipe out coral cover over a large area in a short period of time (Colgan 1987). A meta-analysis based on 2,258 surveys of 214 GBR reefs from 1985 to 2012 documented declines in coral cover from 28% to 14%, 42% of which was attributable to COTS outbreaks (De'ath et al. 2012). The specific causative mechanisms that drive COTS outbreaks remain unknown, with considerable debate in the scientific literature about whether outbreaks in recent decades are more of a human-induced phenomenon as a result of sedimentation and urbanization, runoff, fishing, or primarily a naturally occurring phenomenon (Brainard et al. 2011).

Although predation is usually a chronic energy drain on corals, acute massive outbreaks of some invertebrate corallivores can occasionally increase the corallivore population by orders of magnitude in a single season. For example, the gastropod *Drupella cornus* quickly increased from 100-200 snails per km^2 of reef to 1–2 million per km^2 in western Australia. COTS populations sometime increase within a few months from a few individuals on a reef to hundreds

of thousands (Brainard et al. 2011). In some areas of the Indo-Pacific, these outbreaks have long been considered to be caused by land-based nutrient runoff that result in phytoplankton blooms which, in turn, provide food for the larvae of the predators and facilitate high recruitment of corallivores (Birkeland 1982). Fishing of the predators of corallivores also has been suggested to contribute to these outbreaks. Increases in nutrient runoff from agricultural activities, coastal construction, and fishing of potential predators of corallivores, are all likely contributing to COTS outbreaks (Fabricius et al. 2010).

Corals are also thought to be indirectly affected by human removal of large apex predators. These predators are often the prime targets of fishers and thus frequently depleted from coral reef ecosystems near human populations. Reefs with larger predatory fishes typically have large herbivore populations (Stevenson et al. 2007) which, in turn, maintain low macroalgal cover. Low macroalgal cover improves the chances for successful coral recruitment. This three-level process is called the trophic cascade effect of removal of top predators. Predatory fishes also control invertebrate corallivores such as *Drupella* and COTS (Dulvy et al. 2004). Therefore, apex predators are probably important for directly controlling corallivores and indirectly controlling macroalgae, which facilitates coral recruitment. Unfortunately, apex predators are now generally common only around remote Pacific islands and atolls where fishing pressure is slight, and in other remote areas of the Indo-Pacific (Brainard et al. 2011).

A review of 328 COTS outbreaks in the Indo-Pacific since the mid-20th century showed outbreaks across the region, with recurrent outbreaks on the GBR, Japan, and French Polynesia since the 1960s (Pratchett et al. 2014). Since 1990, 246 outbreaks were recorded, which was triple the number of outbreaks reported (82) prior to 1990. Because of the increase in coral reef surveys and monitoring since 1990, this apparent increase in the number of reported outbreaks may or may not indicate a real increase in outbreaks. In locations where there have been recurrent outbreaks, there was no evidence of increased frequency of outbreaks. If anything, the period between successive outbreaks had become longer, as might be predicted if the initiation of renewed outbreaks requires substantial recovery of coral prey (Pratchett et al. 2014).

Projected Effects of Predation. Because human populations near coral reefs in much of the Indo-Pacific are expected to grow, it is likely that fishing, land-based sources of pollution, and other human impacts to coral reefs will increase throughout most of the Indo-Pacific in the foreseeable future. These, in turn, are very likely to contribute to increased chronic and acute predator (corallivore) outbreaks by the mechanisms discussed above. As predation on corals becomes more frequent, the decrease in coral reproductive stock and larval production could result in depensatory effects on a large scale. Depensatory effects refer to a progressively lower likelihood of individual coral colony survival due to an increasing predator population and a decreasing coral population, which could cause the impacts of predation to increase exponentially (Brainard et al. 2011).

Predation Conclusion. From the above analysis of predation on Indo-Pacific reef-building corals, we conclude that (1) both chronic and acute predation, especially acute COTS outbreaks, have been observed in many parts of the Indo-Pacific and, while quantifiable temporal trends are lacking, environmental stressors that lead to predator outbreaks (e.g., land-based sources of pollution) have increased; and (2) both chronic and acute predation and its impacts are projected to increase in much of the Indo-Pacific in the foreseeable future.

4.2.8.   Collection and Trade (Factor B)

Collection and trade refers to the physical process of taking reef-building corals from their natural habitat (collection) for the purpose of sale in the marine aquarium and ornamental

industries (trade), and thus is considered under ESA Factor B – overutilization for commercial, recreational, scientific, or educational purposes. Artificial propagation of corals also plays a part in this threat or the mitigation of it. Collection and trade threaten corals by directly removing individual colonies from populations, and indirectly by altering or destroying coral habitat during the collection process. In order to adequately describe this threat, we provide summaries of (1) observed effects of collection and trade of Indo-Pacific reef-building corals to date; (2) projected effects of collection and trade of Indo-Pacific reef-building corals in the foreseeable future

      <u>Observed Effects of Collection and Trade</u>. We define wild collection as the physical removal of coral colonies and fragments from their natural habitat. We discuss coral aquaculture and mariculture that is done for the purposes of trade here, because captive culture techniques are increasingly used to supply the marine aquarium industry and potentially reduce the amount of corals collected from the wild to meet demand. Globally, 1.5 million live stony coral colonies (i.e., corals with hard skeletons, including both reef-building and non-reef-building species) were reported to be collected from at least 45 countries each year between 1988 and 2007, with the great majority from the Indo-Pacific due to undesirable appearance and growth characteristics of Caribbean corals for trade. The U.S. consumed the largest portion of live corals and live rock, followed by the European Union and Japan. The imports of live corals taken directly from coral reefs (not produced by aquaculture or mariculture) increased by 600% between 1988 and 2007, while the global trade in live coral increased by nearly 1,500%. Harvest of corals from their natural habitat is usually destructive to the reef habitat around the corals, and also can result in removing and discarding large amounts of live coral that go unsold. While collection is typically focused on small parts of a coral reef, it can result in significant impacts to that reef and may contribute to individual species' extinction risk (NMFS 2014).

      Recently, advances in both aquaculture (land-based) and mariculture (ocean-based) captive culture techniques show promise in shifting the demand of the marine aquarium industry away from wild-collected corals to corals reared via captive-culture techniques. Such techniques are possible since many corals, especially fast-growing branching corals, are capable of asexual reproduction via a process known as fragmentation or "fragging" (Rhyne et al. 2012). The proportion of the live coral trade supplied by captive culture instead of wild collection is difficult to track and calculate, with the most recent estimates ranging from 2% (Thornhill 2012) to 20% (Wood et al. 2012). However, the proportion appears to be increasing, as major exporters such as those from Indonesia, Fiji, and the Solomon Islands switch from wild collection to mariculture (Rhyne et al. 2014), as described in more detail below.

      Globally, there are approximately two million aquarium hobbyists involved in a complex trade network that sells an estimated 50 million stony and soft corals every year, the great majority of which are artificially propagated (Rhyne et al. 2012). According to the Florida Department of Agriculture and Consumer Services, there are 87 certified aquaculture facilities listing corals (mostly Indo-Pacific reef-building corals) as a product in Florida alone. Since 2000, Indonesia has been the primary source of live corals, exporting approximately one million corals annually and represented an estimated 91% of the global supply market as of 2005 (Bruckner and Borneman 2006, Timotius et al. 2009, Thornhill 2012). Other major sources of scleractinian corals include Fiji, Solomon Islands, Tonga, and Australia. In addition, undocumented, illegal live coral trade is estimated to represent approximately 25% of the legal trade level, although these numbers are difficult to estimate considering the secretive nature of the illegal trade (Jones 2008, Thornhill 2012). In addition to increasing wild collection of corals, some major source countries such as Indonesia are increasing production via mariculture activities to reduce wild

collection pressure on coral reefs, and supporting coral farming as a potential alternative to fishing for reef fish and collection of wild corals (Pomeroy et al. 2006). As of 2008, there were 55 coral farms scattered throughout the different provinces of Indonesia (Timotius et al. 2009), and the majority of Indonesia's live coral exports were produced by mariculture by 2009 (Rhyne et al. 2014). According to 2009 U.S. import reports, 26% of *Acropora* species were identified under CITES codes which indicated that these colonies were produced at aquaculture facilities (Rhyne and Tlusty 2012).

The export of marine organisms for the marine aquarium and ornamental trade is a global industry. In addition to live stony corals, approximately 13–40 million reef fish, four million pounds of dead coral skeleton, and 9–10 million other invertebrates are extracted from coral reef ecosystems across the world every year (Thornhill 2012). For corals, trade can be broken down into several categories, including coral rock (i.e., rock and substrate that may have live settled coral polyps among other marine organisms), live wild coral, live artificially propagated coral, and dead coral skeleton. Yet, numbers of corals traded in these categories are very difficult to accurately estimate for several reasons: (1) corals are colonial, vary in size, and can be fragmented into many smaller pieces; (2) reporting of trade volume is inconsistent and varies between reporting pieces and weight; and (3) live rock and corals are often confused with each other and misreported (Thornhill 2012).

The ten most popular coral genera involved in the global marine aquarium trade by volume are *Acropora* (Indo-Pacific only)*, Euphyllia, Goniopora, Trachyphyllia, Plerogyra, Montipora, Heliofungia, Lobophyllia, Porites*, and *Turbinaria* (Jones 2008, Thornhill 2012), all of which are Indo-Pacific reef-building corals. *Acropora* species are in the highest demand followed by the large polyp species such as *Euphyllia* (Jones 2008).

Projected Effects of Collection and Trade. Because human populations near coral reefs in much of the Indo-Pacific are expected to grow, and collection and trade is fueled by the world's current demand for marine aquaria in the U.S., the European Union, and Japan which is expected to grow, collection and trade of corals is likely to grow into the foreseeable future. On top of that, because the economic middle and upper classes in Asia are growing so quickly, 88% of the next billion members of the middle class are projected to be from eastern and southern Asia (Kharas 2017). This rapid growth in potential consumers of luxury items is likely to drive up demand for marine aquaria in Asia, in addition to the current and growing demand in the U.S., the European Union, Japan, and elsewhere. Therefore, it is likely that collection and trade will increase throughout most of the Indo-Pacific in response to the growing global demand, which in turn is likely to result in increased detrimental effects to Indo-Pacific reef-building corals, although these effects may be partially offset by increases in captive culture.

Collection and Trade Conclusion. From the above analysis of the effects of collection and trade on Indo-Pacific reef-building corals, we conclude that (1) wild collection and aquaculture production of Indo-Pacific reef-building corals has grown significantly in recent decades, along with the resulting detrimental effects to corals and their habitats; and (2) the industry and its effects are projected to increase in much of the Indo-Pacific in the foreseeable future, although these effects may be partially offset by increases in captive culture.

4.2.9.   Other Threats

In addition to the above primary threats, other threats to Indo-Pacific reef-building corals include two global threats (changes in ocean circulation and tropical storms), and three local threats (human-induced physical damage, invasive species, and salinity; Brainard et al. 2011). These are not considered primary threats because they are either uncertain (the global threats) or

highly localized on small spatial scales (the local threats). Nevertheless, they may affect the extinction risk of some Indo-Pacific reef-building coral species in the foreseeable future and, therefore, are briefly described below. The ESA Factor is provided in parentheses for each threat.

Changes in Ocean Circulation (Factor E). Ocean currents directly and significantly influence coral reef ecosystems through many important processes, including heating and cooling, larval connectivity, and nutrient enrichment. The major components of ocean currents influencing coral reefs are wind-driven surface ocean currents, the large-scale density-driven thermohaline circulation of the ocean interior, tidal currents, and wave-driven nearshore currents. East to west tropical currents are driven by the overturning of air across the equatorial oceans known as the Walker Circulation, which has shown signs of weakening in recent decades. Projected changes to oceanic circulation in the Indo-Pacific are strongly dependent on future changes in the Walker Circulation. AR5 concluded that there is medium confidence that weakening of tropical Pacific ocean circulation will occur in the foreseeable future. Such basin-scale ocean circulation changes could have significant and far-reaching consequences for Indo-Pacific reef-building corals and other marine life. For example, weakening circulation could reduce coral connectivity between reefs, which is essential for providing larvae to foster recovery from disturbance as well as long-term gene flow (Brainard et al. 2011, IPCC 2013).

Changes in Tropical Storms (Factor E). Tropical storms (hurricanes, typhoons, or tropical cyclones) are one of the many forms of natural disturbance that Indo-Pacific reef-building corals have experienced throughout their existence. Tropical storms cause direct physical damage to corals by colony abrasion, breakage, and uprooting, as well as by increasing sediment, debris, and turbidity on reefs, which together typically lead to sharp but localized and temporary reductions in coral cover. Tropical storms can also benefit corals by cooling seawater temperatures and facilitating asexual reproduction. However, human disturbances to these coral reef ecosystems have reduced their capacity to recover from tropical storms (Brainard et al. 2011). Global climate change may be changing the frequency, intensity, and spatial distribution of tropical storms. Although the frequency of tropical storms does not appear to have increased in the Indo-Pacific (as it has in the Atlantic), there is evidence that the intensity of tropical storms in the Indo-Pacific has increased in recent decades. Over the first half of the 21st century, AR5 projects no change in the frequency of tropical storms in the Pacific, but does project increases in their intensity. That said, both the frequency and intensity projections have low confidence. AR5 also projects that frequency, intensity, and spatial distribution of tropical storms will be highly variable throughout the 21st century globally (IPCC 2013, Table 11.2).

Human-induced Physical Damage (Factor A). Physical damage to corals by human activities is distinct from storm-induced physical damage, in that it tends to be much more frequent, but individual incidents are on much smaller scales. Humans inflict physical damage on coral reefs through both intentional use and accidents. Intentional use includes a diverse array of coastal construction and development activities, including land reclamation, airport and harbor construction, navigation channel dredging, mining for building materials, and other activities. Accidental damage occurs from vessel groundings, anchoring, fishing gear, recreation (e.g., trampling, breakage, and other damage from snorkeling and diving), and other activities (Brainard et al. 2011). All of these human activities have increased rapidly in the Indo-Pacific over the last several decades, as coastal development, economic growth, and technological advancements have all proceeded across the region. Projected human population growth and economic development virtually guarantees that human-induced physical damage of Indo-Pacific coral reefs will continue and likely increase throughout the foreseeable future.

Invasive Species (Factor E). Introduced marine invertebrate species, along with their associated diseases and symbionts, have been spreading through the Indo-Pacific for at least decades, if not centuries. This is substantially increasing the number of marine invertebrate species in some harbors, especially in the more isolated archipelagoes, and tends to homogenize marine biogeography. The transportation of introduced marine invertebrate species is most often by ship, either on the hull or in the ballast water, and the alien species usually become associated with the ship when it is at rest. This means the departure and arrival of introduced species is most often in protected ports or harbors, thus introduced marine invertebrates tend to originate from such areas, and are often not able to colonize habitats outside of ports or harbors. For example, in Guam there are 79 species of introduced marine invertebrates in Apra Harbor, but only 23% have been found outside the harbor, and those few that have made it outside the harbor have so far been ecologically inconsequential on the open coast coral reefs (Paulay et al. 2002). In Hawaii, there are 287 introduced marine invertebrate species, but a large portion of these are found in Pearl Harbor and relatively few have become established on the wave- exposed outer reefs (Eldredge and Smith 2001). In some cases, alien species introductions are not accidental. For example, some of the algal species that have become invasive in Hawaii were introduced deliberately for aquaculture because of their characteristics of rapid growth and productivity. The main impact of introduced invertebrates and algae is that they are often able to outcompete the slower -growing corals for space (Brainard et al. 2011). Projected human population growth and economic development will likely result in growth in the shipping industry in the Indo-Pacific, which in turn makes it likely that marine invasive species will continue to be introduced to Indo-Pacific coral reefs in the foreseeable future.

Salinity (Factor A). Nearshore coral reef habitats like reef flats, lagoons, and fringing coral reefs can experience extreme salinity changes. Evaporation during extreme droughts and during windy, hot conditions on shallow banks can produce hypersaline waters, while hyposaline water is released into the coastal zone following heavy rain, and can persist for several weeks or longer. For coastal reefs, heavy rain drives coastal runoff or groundwater inputs, both of which can bring other associated stresses (see Land-based Sources of Pollution above). Coral responses to salinity are, in part, controlled by behaviors, such as polyp retraction, mucus production, and osmoregulation. High and low salinity can influence corals during many life stages. Severe rain events can produce catastrophic local coral bleaching. For example, a single storm in 1987 reduced the salinity in parts of Kaneohe Bay, Hawaii to 15 parts per thousand, causing mass mortality to *Pocillopora damicornis* and *Montipora verrucosa* at depths of 2 m (Jokiel et al. 1993). A general response of corals to reduced salinity is mucus formation, tissue swelling, and reduced photosynthesis (Brainard et al. 2011). Most salinity stresses to corals are driven by rainfall, and can be a type of land-based source of pollution if caused by runoff. Salinity stress has likely increased along with other land-based sources of pollution in the Indo-Pacific, in response to watershed and coastal development that has increased runoff. Such development is projected to increase rapidly in many parts of the Indo-Pacific, thus salinity effects on Indo-Pacific reef-building corals will likely increase in the foreseeable future.

4.2.10.   Interactions of Threats

The threats described above often affect Indo-Pacific reef-building corals simultaneously or sequentially, thus threats may interact with one another to affect corals in different ways than they would individually. Because of the large number of threats to Indo-Pacific reef-building corals, and the fact that multiple threats can interact with one another, there are many types of potential interactions (Anthony et al. 2016, Ateweberhan et al. 2013). Some of the most

important interactions of threats that have been observed in the Indo-Pacific are: (1) ocean warming causes coral bleaching, and bleached corals are more susceptible to diseases (McClanahan et al. 2009, Burge et al. 2014); (2) corals with reduced calcification are more sensitive to bleaching and diseases (Anthony et al. 2011, 2016); (3) coral skeletons weakened by ocean acidification are more sensitive to the impact of predators and storms (Anthony et al. 2011, 2016); (4) turbidity can increase susceptibility to bleaching (Hongo & Yamano 2013) but also decrease bleaching by blocking light (Morgan et al. 2017); (5) sedimentation hinders recovery from bleaching by smothering corals and limiting settlement of coral larvae (Fabricius 2011); (6) elevated nutrients reduce coral capacity to combat stress, leading to increased warming-induced bleaching (Wooldridge 2009, 2016); and (7) sedimentation and elevated nutrients exacerbate coral diseases in numerous ways (Heron et al. 2012, Lamb et al. 2016).

As described above, all threats are projected to worsen in the foreseeable future (i.e., from now to 2100), thus it is highly likely that the effects of the interactions of these threats will also worsen. This is borne out by the following studies on the interaction of ocean warming with one other major threat: An analysis of the likely reef coral disease outbreaks resulting from ocean warming projected by RCP4.5 and RCP8.5 concluded that both pathways are likely to cause sharply increased, but spatially highly variable, levels of coral disease in the future, and that the outbreaks would be more widespread, frequent, and severe under RCP8.5 than RCP4.5 (Maynard et al. 2015). An analysis of the responses of coral reefs to increased ocean warming and acidification under all four pathways found that only RCP2.6 would allow the current downward trend in coral reefs to stabilize, and that RCP4.5 would likely drive the elimination of most coral reefs by 2040–2050 (Hoegh-Guldberg et al. 2017), implying that RCP8.5 would be even worse. These studies oversimplify the interactions of threats by only considering interactions of two threats. The reality is that most or all threats interact with one another at various spatial and temporal scales, thus the effects of these interactions could be significantly worse than any individual threat alone, especially as each threat grows in the foreseeable future. Therefore, the above descriptions of the projected effects of individual threats on Indo-Pacific reef-building corals in the foreseeable future may understate the combined effects of all threats together.

4.3. Inadequacy of Existing Regulatory Mechanisms (ESA Factor D)

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

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

Twenty countries, the "G20" nations, are responsible for approximately 78% of global emissions, and are led by the top three emitters, China, the U.S., and India, which are together responsible for about half of global emissions (UNEP 2018, 2019). All 20 signed the Paris Agreement; however, in 2017, the US announced its withdrawal, to take effect in late 2020. Each of the 195 signatories of the Paris Agreement is required to develop "Nationally Determined Contributions" (NDCs) under the agreement that specify national GHG reduction targets and how they will be met. Each signatory was supposed to submit its NDCs to the UNFCCC and begin implementation no later than 2020. According to the UNFCCC's NDC Registry, 186 countries had submitted NDCs by early 2020 (https://www4.unfccc.int/sites/ndcstaging/Pages/Home.aspx, accessed February 2020). The United Nations Environmental Programme's (UNEP) annual Emissions Gap Reports (EGRs) monitor the implementation of the Paris Agreement, in order to quantify the gap between the likely outcome of current policies on global warming over the 21st century vs. the agreement's objective of limiting global warming over the 21st century to 1.5° C (i.e. the "emissions gap"). The most recent EGR from November 2019 (UNEP 2019) reports that 13 of the G20 countries are on track to meet their NDC pledges for 2030, but seven are not. More worrisome is that only a few countries had formally submitted long-term strategies to the UNFCCC for achieving net zero GHG emission targets 2050. The 2019 EGR concluded that current policies are on track to result in global warming of 3.5° C by 2100 (UNEP 2019), far short of the Paris Agreement's objective of limiting global warming to well under 2.0° C by then.

The Montreal Protocol successfully reduced ozone-depleting substances, leading to recovery of the ozone layer and a modest reduction in secondary GHGs (NMFS 2012). However, the Kyoto Protocol has not been effective at controlling global GHG emissions, because many of the top GHG emitters did not sign the protocol, and some who did were unable to ratify the protocol or implement it as intended. As a result, atmospheric CO_2 concentrations increased from

approximately 360 ppm to 390 ppm during the time the protocol was in effect from 1997 to 2012 (https://www.esrl.noaa.gov/gmd/ccgg/trends/, accessed February 2019), due to the steady increase in GHG emissions during that time (IPCC 2013, IEA 2017). The Copenhagen Accord represented some progress but was only intended as a non-binding interim step until a more permanent binding agreement could be completed, which was done in Paris in 2015 and signed by 195 countries in 2016. However, even if implementation of the Paris Agreement successfully limits global temperature increases to 1.5° C during the 21st century as intended (i.e., 0.5° C warmer than now), this would likely result in very high risk of severe impacts to coral reefs, assuming that corals do not further acclimatize or adapt to the projected warming (Fig. 3-18, IPCC 2018). That is, severe impacts are anticipated from only an additional 0.5° C of additional warming above current levels because coral reefs are already on a downward trajectory, and the additional warming would make things worse (IPCC 2018).

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

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

Coral collection and trade regulatory mechanisms include specific laws that prohibit the collection, harvest, and mining of corals. In some instances, these coral collection regulatory mechanisms are limited in scope because they apply only to certain areas, or are regulated but not prohibited. Of the 68 countries, 32 (47%) have laws prohibiting the collection of live corals from coral reefs. In addition, at least one international regulatory mechanism helps reduce the collection of live corals, the Convention on International Trade in Endangered Species of Wild Flora and Fauna (CITES), which restricts trade of species listed in any of its three categories. Nearly all reef-building corals are listed in CITES Appendix II, which requires export permits but not import permits. These national and international regulatory mechanisms address the

threat of collection and trade, but in many countries and locales, the laws are not well enforced (NMFS 2012, NMFS 2014).

Fishing regulations that pertain to reefs, include regulations that prohibit explosives, poisons and chemicals, electrocution, spearfishing, specific mesh sizes of nets, or other fishing gear. Fisheries management regimes regulate reef fishing in many parts of the collective ranges of these coral species, albeit at varying levels of success. Of the 68 countries, 53 (68%) have laws that regulate coral reef fisheries. Although these laws are very diverse, they all prohibit destructive fishing practices, especially the use of dynamite or otherwise deconstructing the reef, while many also prohibit the use of poisons. Many of the 53 countries entirely prohibit spearfishing while scuba diving at night when reef fish are much more vulnerable. Some of the 53 countries prohibit or regulate fishing nets and traps on coral reefs. There are no international regulatory mechanism that address coral reef fisheries. These national regulatory mechanisms address the threat of fishing, but in many countries and locales, the laws are not well enforced (NMFS 2012, NMFS 2014).

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

Managed area regulatory mechanisms include the capacity to create national parks and reserves, sanctuaries, and marine protected areas (NMFS 2012, NMFS 2014). As of 2011, coral reef marine protected areas (MPAs) included approximately 25% of Indo-Pacific coral reefs (Burke et al. 2011), thereby reducing some threats through regulation or banning of fishing, coastal development, and other activities contributing to local threats. Since then, several new coral reef MPAs were established that slightly increase the proportion of protected Indo-Pacific coral reef ecosystems. In 2014, New Caledonia established the multiple-use Coral Sea Natural Park covering its entire Exclusive Economic Zone (EEZ), including some coral reefs in MPAs that were designated as no-take zones in 2018 (MPA News 2018). In 2017, the Cook Islands established the multiple-use Marae Moana Marine Park covering its entire Exclusive Economic Zone (EEZ), including all of its approximately 1,100 km^2 of coral reefs where fishing and other commercial activities are restricted. In Palau and parts of the U.S. Pacific Islands in 2015 and 2016, respectively, EEZs surrounding previously-protected coral reef waters were established as no-take MPAs, bolstering conservation of the coral reef ecosystems within (Lewis et al. 2017). While increasing the proportion of Indo-Pacific coral reefs within MPAs is a positive step, inclusion in MPAs does not guarantee that coral reefs are protected from local threats: Only

about 15% of MPAs with Indo-Pacific coral reefs were rated as "effective" at protecting the coral reefs within them from local threats in 2010 (Burke et al. 2011), and MPAs are generally not very effective at protecting coral reefs from the climate change threats (Bruno et al. 2019).

Regulatory Mechanisms Conclusion. The 2014 final coral listing rule concluded that global regulatory mechanisms for GHG emissions management were ineffective at reducing global climate change-related impacts to Indo-Pacific reef-building coral species at that time (NMFS 2014). Since then, the 2015 Paris Agreement was signed by 195 countries, representing a major potential advance in GHG emissions management because its successful implementation would limit GMST to 1.5° C above pre-industrial, as explained in the Global Climate Change section above, and in IPCC's 1.5° C Report (IPCC 2018). However, there are several reasons why there is cause for pessimism with regard to successful implementation of the Paris Agreement: (1) Despite past international agreements for GHG emissions management (e.g., 1997 Kyoto Protocol, 2009 Copenhagen Accord), global GHG emissions and atmospheric CO_2 levels have both risen to historically high levels and continue to do so; (2) the world's second largest GHG emitter, the U.S., has announced its withdrawal from the Paris Agreement in late 2020; and (3) recent analyses shows that about half of the G20 nations were already falling short of the commitments they made in the Paris Agreement (UNEP 2018, 2019). Finally, even successful implementation of the Paris Agreement, which would result in fewer impacts to Indo-Pacific reef-building corals than RCP8.5, would result in a worsening of the current conditions, as explained in the Ocean Warming section above. Thus, we conclude that current global regulatory mechanisms for management of GHG emissions are expected to be unsuccessful at reducing global climate change-related impacts to Indo-Pacific reef-building corals.

The 2014 final coral listing rule concluded that national, state, local, and other regulatory mechanisms in the 68 countries with Indo-Pacific reef-building corals were generally ineffective at preventing or sufficiently controlling local threats to these species (NMFS 2014). Since that time, new coral reef MPAs have been established in the Indo-Pacific as described above, slightly increasing the total proportion of coral reef ecosystems protected by MPAs in the region. However, human populations have also grown in many Indo-Pacific countries during that time, as described in the fishing section of the Threats Evaluation above, most likely leading to an increase in local threats since we completed our analysis in 2014. Thus, we conclude that current regulatory mechanisms are still ineffective at reducing the impacts of local threats to Indo-Pacific reef-building corals.

4.4. Threats Evaluation Conclusion

As described in detail above, we consider global climate change-related threats of ocean warming, ocean acidification, and sea-level rise, and the local threats of fishing, land-based sources of pollution, coral disease, predation, and collection and trade, to be the most important to the extinction risk of Indo-Pacific reef-building corals currently and in the foreseeable future. The most important of these is ocean warming. In addition, five lesser global and local threats are also described (changes in ocean circulation, changes in tropical storms, human-induced physical damage, invasive species, and salinity). The interactions of threats with one another could be significantly worse than any individual threat, especially as each threat grows. Each threat, and the interactions of threats, are described both in terms of observed effects since relevant scientific information became available (usually mid-20th century), and projected effects over the foreseeable future, as summarized in Table 6 below. The inadequacy of existing regulatory mechanisms has exacerbated all threats.

The effects of all threats except sea-level rise, coral disease, coral predators, changes in ocean circulation, and tropical storms on Indo-Pacific reef-building corals have already been observed to be worsening, based on the monitoring results and the scientific literature cited above. Ocean warming in conjunction with the other threats has recently resulted in the worst impacts to Indo-Pacific reef-building corals ever observed. These impacts are further described in terms of disturbance, recovery, coral cover, and resilience in the trends section above. Unfortunately, all threats are projected to worsen in the foreseeable future, based on the scientific literature, IPCC climate change models, and other information (e.g., human population trends in the Indo-Pacific) cited above, and summarized in Table 6 below. The inadequacy of existing regulatory mechanisms is expected to exacerbate all threats.

Table 6. <u>Summary of Threats Evaluation</u>. Observed and projected trends of effects of threats on Indo-Pacific reef-building corals.

Threat	Observed*	Projected*
Effects of Ocean Warming	↑	↑
Effects of Ocean Acidification	↑	↑
Effects of Sea-level Rise	O	↑
Effects of Fishing	↑	↑
Effects of Land-based Sources of Pollution	↑	↑
Effects of Coral Disease	O	↑
Effects of Predation	O	↑
Effects of Collection and Trade	↑	↑
Effects of Other Global Threats	O	↑
Effects of Other Local Threats	↑	↑
Effects of Interactions of Threats	↑	↑

* Observed = from mid-20th century to present. Projected = from present to 2100. ↑ = a negative upward trend. O = available information does not indicate any trend.

5. Literature Cited

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