

3. THREATS TO CORAL SPECIES

3.1 Human Population

This chapter describes a multitude of threats or stressors that affect coral populations and contribute varying degrees of extinction risk. The common root or driver of most, possibly all, of these threats is the number of humans populating the planet and the level of human consumption of natural resources, both of which are increasing in most areas around the globe. The combination of increasing numbers of humans and their persistently rising per capita resource demands are directly responsible for escalating atmospheric CO₂ buildup and associated impacts, both direct (e.g., ocean warming, ocean acidification, and sea-level rise) and indirect (influential in the increased prevalence of many coral diseases, decreased ability of corals to deposit calcium carbonate skeletons, increased energy for storms, and the potential of increased input and resuspension of coastal sediments by changing precipitation patterns or sea-level rise). Increased human population and consumption of natural resources are also root causes for increases in fishing (particularly of herbivores) at many locations around the globe, for massive inputs of nutrients (eutrophication), toxic pollutants, and sediments into many coastal waters, and for the spread of invasive species. A recent study by Mora (2008) specifically attributed variation in condition of several reef guilds, including coral mortality, to adjacent human population densities across the Caribbean; similar effects have been correlated with watershed development indices (Oliver et al., 2011). Coral reefs, along with other natural systems, are continuing to deteriorate around the world, despite the committed efforts of international, national, and local governments and more than 450 nongovernmental organizations worldwide to better manage and conserve coral reefs (Wilkinson and Souter, 2008; Burke et al., 2011). The BRT's evaluation of the current status of the 82 candidate coral species includes consideration of existing observable trends in threats to corals. Trends in human population size and resource demands, which are the ultimate drivers of both global and local threats, were important factors in our assessment of whether the key proximate threats (e.g., climate change, sedimentation, etc.) will increase or decline over the next century.

The relationship between human population size, consumption, and environmental impact has been described using the equation $I=P \times A \times T$, where “I” is the environmental impact, “P” is the human population size, “A” is population affluence, and “T” is technology (Commoner et al., 1971; Ehrlich and Holdren, 1970; 1972; Ehrlich and Holdren, 1971). While more elaborate versions of the model have been developed (Rosa et al., 2004; York et al., 2003), even in this simple form the model is useful as a heuristic framework for understanding the effect of people on the environment. Anthropogenic stressors, which include human-caused climate change and a diverse array of local direct impacts, are a function of the number of people there are, the amount of natural resources each of them use (“affluence”), and the technologies used to extract and consume the resources. However, the relationship may not be strictly multiplicative as described in the IPAT equation, and quantifying terms like “affluence” or “technology” in a common currency have proven to be challenging. In many regions and demographic sectors, the growth of consumption is emerging as the dominant factor increasing anthropogenic pressure on the environment. While world population has grown at a rate of 1.2% per year in recent decades, globally averaged income per person has grown at a rate of 1.4% per year (World Bank, 1999). Assuming income is directly related to consumption, consumption growth has already surpassed human population growth in our rising demand for resources and deleterious environmental outcomes. Population and consumption combined determine the level of human demand for natural resources, but the way in which demand is satisfied—the chosen technologies—is also crucial. As a general rule, most technologies that were sustainable when first introduced became unsustainable as human population densities and consumption levels increased (Harrison and Pearce, 2000).

3.1.1 Human population status and trends

The number of humans in proximity to coral reefs is a key predictor of Caribbean reef status (Mora, 2008) and human population distribution is a primary indicator of local threats to coral reefs worldwide (Burke et al., 2011). The BRT examined the trends in human population abundance at both the global scale, which affects global threats from carbon emissions, and at regional scales, which more often affects local threats to corals.

The current human population (Feb. 4, 2011) around the globe is estimated to be 6.9 billion (U.S. Census Bureau). Human population has experienced continuous growth since around the year 1400, with dramatic increases since the Industrial Revolution (Table 3.1.1). Whereas it took all of human history until 1804 for world human population to reach one billion, the second billion was achieved in only 123 years (1927), the third billion in 33 years (1960), the fourth billion in 14 years (1974), the fifth billion in only 13 years (1987), and the sixth billion in 12 years (1999) (Population Reference Bureau, 2010). During the 20th century alone, the world saw the largest increase in its population

in human history (from 1.65 billion to 6 billion) because of medical advances and massive increases in agricultural productivity through the mid-1900s, and decline of the mortality rate in many countries.

Table 3.1.1. Years of occurrence and years elapsed for human population to reach each additional billion people. For instance, the human population first reached 1 billion in 1804 and 2 billion in 1927, so it took 123 more years to reach second billion. Source: Population Reference Bureau 2010.

World population estimates milestones

Population (in billions)	1	2	3	4	5	6	7	8	9
Year	1804	1927	1960	1974	1987	1999	2011	2025	2045–50
Years elapsed	123	33	14	13	12	12	14	20–25	

The highest rates of human population growth occurred briefly during the 1950s, then for a longer period during the 1960s and 1970s (Population Reference Bureau, 2010). The growth rate peaked at 2.2% in 1963, and declined to 1.1% by 2009. Annual births have dropped to 140 million since their peak at 173 million in the late 1990s and are expected to remain nearly constant, while deaths number 57 million per year and are expected to increase to 90 million per year by 2050. Current projections show a steady decline in the population growth rate (Fig. 3.1.1), with the population expected to reach between 8 and 10.5 billion between the year 2040 and 2050 (DESA, 2009).

Global human population is projected to reach seven billion by late 2011, and around eight billion by 2025. By 2045–2050, the world’s population is currently projected to reach around 9 billion, with alternative scenarios ranging from 7.4 billion to 10.6 billion (DESA, 2003; 2004; U.S. Census Bureau, 2010). For the purposes of this Status Review Report, the BRT assumed continued declines in growth rates and middle-of-the-road projections of around 9–11 billion people by the year 2100, but recognizing the uncertainties of these projections. This range of human population projections was used to qualitatively inform the BRT of potential future changes in the levels of certain anthropogenic threats.

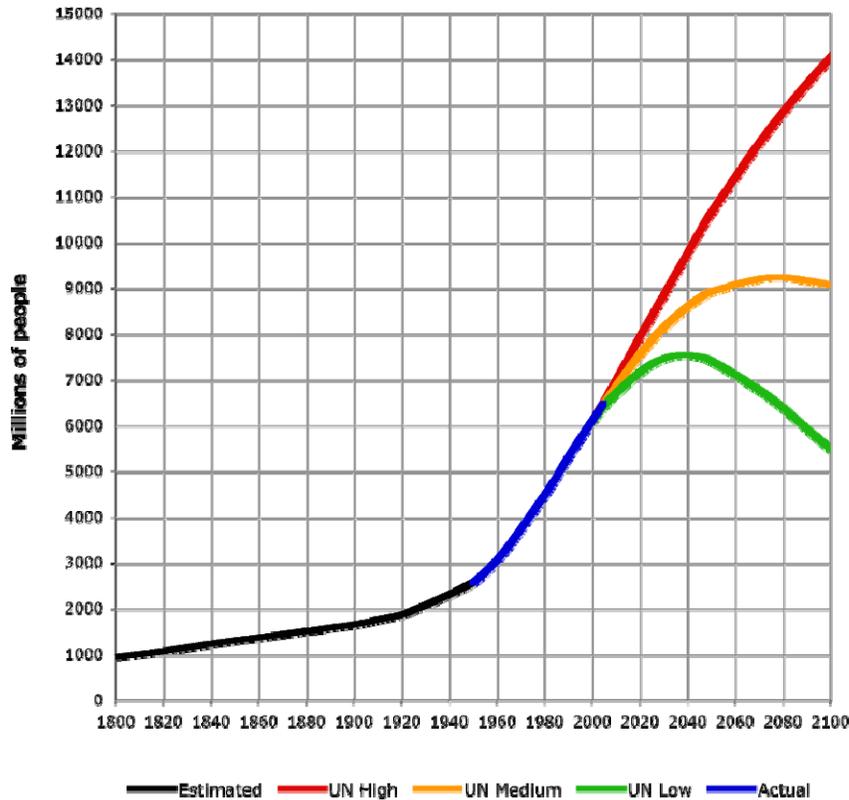


Figure 3.1.1. World population from 1800 to 2100 based on UN 2004 projections (red, orange, green) and U.S. Census Bureau historical estimates (black) and assessments (blue).

While global trends in human population provide indications of global impacts, regional trends in human population provide indications of pressures on regional and local scales. The BRT examined the recent human population abundance time series developed by assigning country-scale human population data to five large geographic regions (Indian Ocean, Caribbean, Southeast Asia, Pacific, and Middle East) that surround and influence the 82 candidate coral species addressed in this Status Review Report (Table 3.1.2). The BRT recognized that data summarized at the country scale probably do not precisely reflect trends in population immediately adjacent to and influencing the 82 candidate coral species examined here, and that it would be useful to examine human population abundance in areas closest to corals as was done in Mora (2008) and Burke et al. (2011). However, time-series data at that scale were not available and the BRT believes that even these regional population scale trends are informative for this review. Between 2005 and 2009, the human population living within 10 km of the coast increased 30% faster than the global average (Burke et al., 2011), suggesting that country-scale data likely underestimate the rate at which the human population in proximity to corals is increasing.

Based on data from the World Bank, human population abundance and density have increased in all five regions since 1960 (Fig. 3.1.2), with the greatest human population densities and increases in population density in the Southeast Asia and Indian Ocean regions. There, current human population densities are 4–5 times greater than the global average and probably suggest the greatest local human-induced effects to corals and coral reefs. In the areas in closest proximity to coral reefs, the Southeast Asian, Indian Ocean and Middle East regions have the highest densities of people per reef area (Fig. 3.1.3; Burke et al., 2011). Since people and their consumption are the root drivers of each of the proximate threats discussed throughout the remainder of this chapter, these trend data suggest increasing risks to corals and coral reefs.

Table 3.1.2. Countries assigned to each of five regions (Indian Ocean, Caribbean, Southeast Asia, Pacific, and Middle East) for regional trend analyses. Note that Mexico, and China were excluded from the analysis because the vast majority of the area of these countries is not adjacent to coral habitats. The States of Florida and Hawai'i were included in the human population abundance and density trends for the Caribbean and Pacific regions, respectively. However, these states were excluded from CO2 emission and land-use analysis (Figs. 3.1.4 and 3.1.5) because state-specific data were not available. Also note that for this analysis the Pacific region does not include countries in the eastern Pacific. Regions and countries are color-coded to match accompanying trend analyses shown in Figures 3.1.2, 3.1.4, and 3.1.5.

Indian Ocean	Caribbean	Southeast Asia	Pacific	Middle East
Kenya	Belize	Thailand	Papua New Guinea	Egypt, Arab Rep.
Mozambique	Colombia	Malaysia	Marshall Islands	Saudi Arabia
Madagascar	Venezuela, RB	Vietnam	Kiribati	Sudan
Seychelles	Aruba	Philippines	Vanuatu	Eritrea
Mauritius	Netherlands Antilles	Singapore	Fiji	Djibouti
Maldives	Trinidad and Tobago	Japan	Samoa	Somalia
India	Cayman Islands	Cambodia	Tonga	Yemen, Rep.
Tanzania	Jamaica		French Polynesia	Oman
Myanmar	Haiti		Solomon Islands	United Arab Emirates
Indonesia	Dominican Republic		Micronesia, Fed. Sts.	Qatar
Comoros	Bahamas, The		Palau	Kuwait
Mayotte	Puerto Rico		Guam	Iran, Islamic Rep.
	Bermuda		New Caledonia	Pakistan
	Virgin Islands (U.S.)		Tuvalu	Jordan
	Antigua and Barbuda		Northern Mariana Islands	Israel
	St. Kitts and Nevis		Hawai'i	
	Dominica			
	St. Lucia			
	Barbados			
	St. Vincent / Grenadines			
	Grenada			
	Florida			

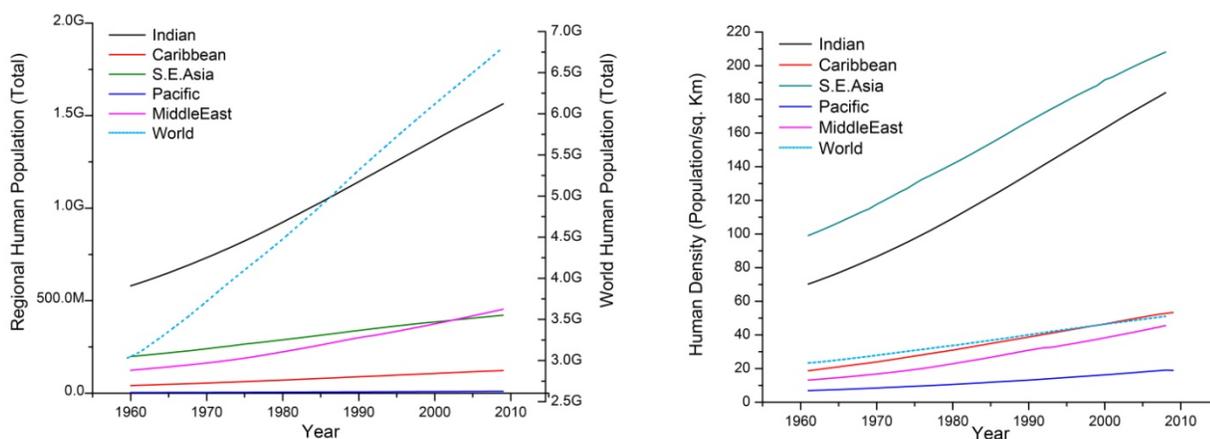


Figure 3.1.2. Recent world and regional trends in (left) human population abundance and (right) human population density from 1960 through 2009. The regional estimates are based on totals for countries listed above (Table 3.1.2), using data from the World Bank online database (World Bank, 2011).

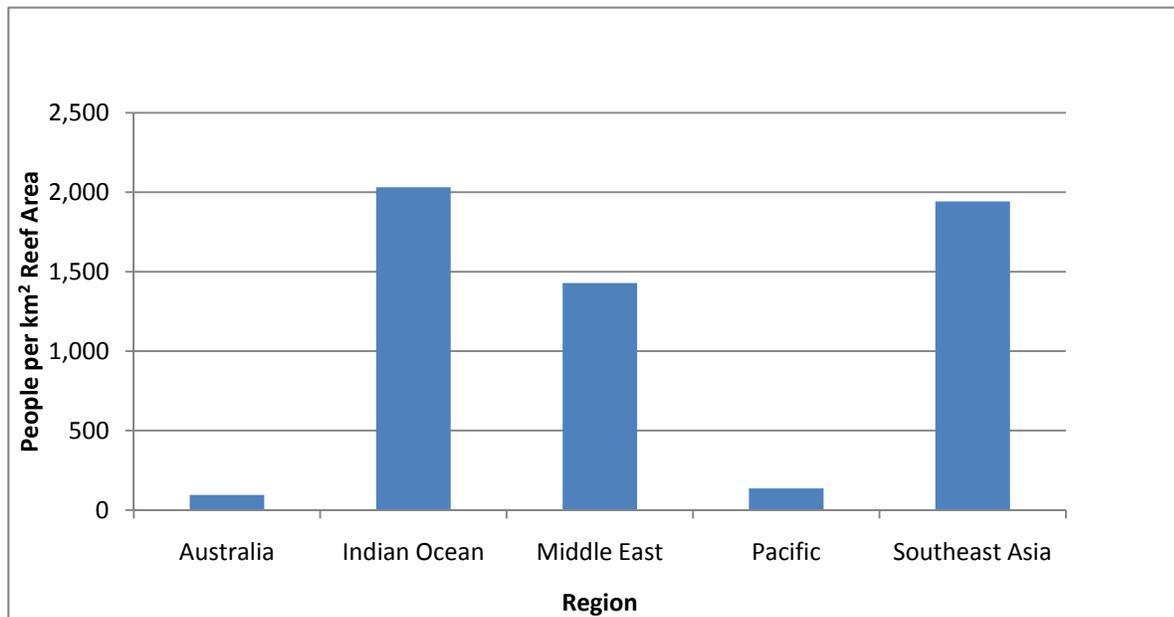


Figure 3.1.3. Approximate number of people living within 10 km of the coast and 30 km of a coral reef per km² of reef. This gives a measure of the population density relative to nearby reefs. Figure constructed from data in Figures 1.1 and 2.1 in Burke et al. (2011).

3.1.2 Consumption status and trends

As the human population continues to increase and the demand for development, infrastructure, and services increases, associated indirect outcomes to corals and coral reefs will occur. Population increases will exert additional pressure on many different types of natural resource consumption. As population increases, the demand for food and materials will continue to increase since people around the globe must be fed, housed, and clothed. Hypothetically, the intensifying use of land and natural resources could, at some point, exceed the capacity of the ecosystems to sustain human needs and lead to resource depletion. In this review, the BRT examined several trends in consumption of resources that affect the sustainability of the 82 candidate coral species. Trends in consumption rates need to be considered at several spatial scales. As described in Section 3.2, per-capita emission of CO₂ and its influences, such as ocean warming and acidification, are key threats that should be considered on a global scale. Other threats, such as land-based sources of pollution (Section 3.3.1) and reef fishing (Section 3.3.4.), need to be considered at more regional and local scales.

Total global CO₂ emissions and global per-capita CO₂ emissions have both been increasing exponentially since the 1960s (Fig. 3.1.4). Of the five regions examined here, the Indian Ocean, Southeast Asia, and Middle East regions have the highest total CO₂ emissions. Per-capita CO₂ emissions are greatest in the Southeast Asia region, followed by the Middle East and Caribbean regions. Not surprisingly, the Pacific region has both the lowest total CO₂ emissions and per-capita CO₂ emissions. With total human population, total global CO₂ emissions, and per-capita CO₂ emissions all increasing, the associated threats to corals and coral reefs are likewise increasing. Although climate change and ocean acidification are driven largely by the total global CO₂ concentrations (see Section 3.2), it is informative to look at regional changes in total and per-capita CO₂ emissions as integrators of human population and affluence. Global and regional CO₂ emission trends are integrative indicators of industrial development and human consumption of natural resources that directly or indirectly affect corals and coral reefs (e.g., road development, production of toxics). Using CO₂ emissions as one indicator of net human consumption, many of the regions influencing the candidate coral species have average per-capita consumption and rates of increase in per-capita consumption substantially greater than the global means.

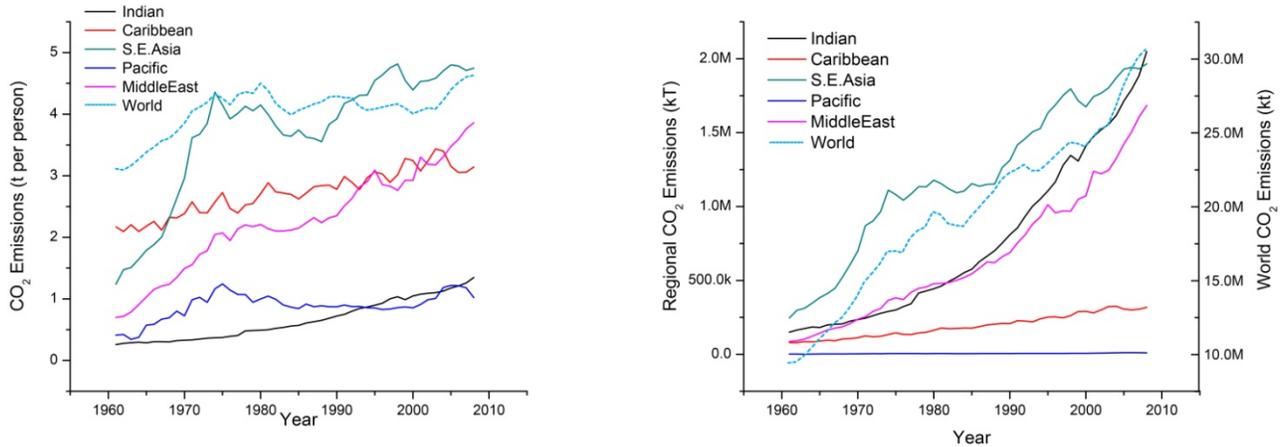


Figure 3.1.4. Recent world and regional trends in (*left*) CO₂ emissions and (*right*) per capita CO₂ emissions from 1960 through 2009. The regional estimates are based on totals for countries listed above (Table 3.1.2), using data from the World Bank online database (World Bank, 2011).

Land-use patterns provide another important indicator and predictor of coral reef status. Large fractions of agricultural land and conversion of natural lands have been associated with numerous negative consequences to coral reefs (Burke et al., 2011; Mora, 2008). The loss of forest cover is also associated with increased sedimentation, which can negatively affect coral reefs (Section 3.3). The Mora (2008) and Burke et al. (2011) papers provide relatively fine-scaled analyses of these changes in relation to human consumption; however, these analyses are largely static snapshots. Figure 3.1.5 show global and regional trends in percent agricultural land area and total forest land area, respectively. The most striking increase in agricultural lands and decrease in forested land area occurred in the Indian Ocean region. The increase in agricultural land area and decrease in forest land area suggests that land-based threats to corals will continue into the future.

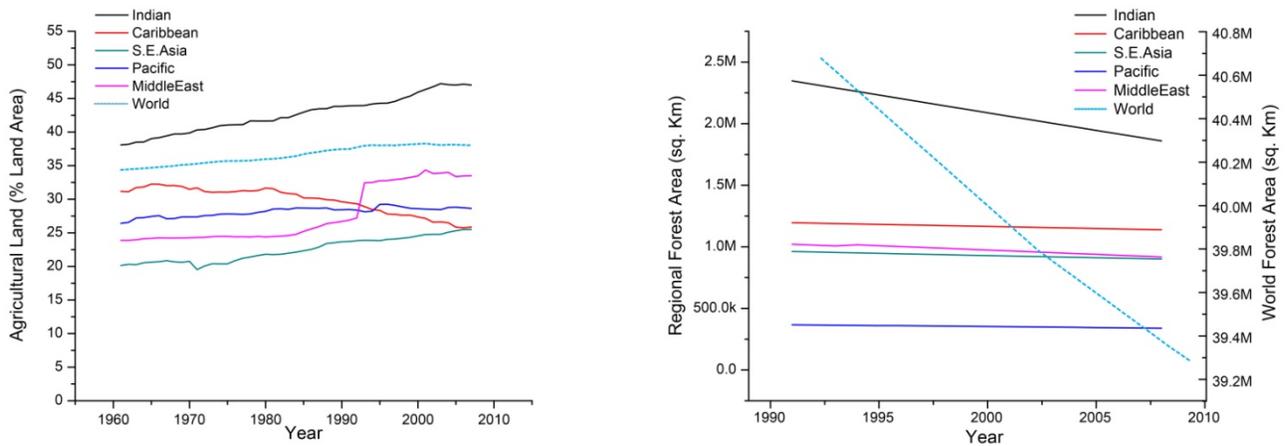


Figure 3.1.5. Recent world and regional trends in percent (*left*) land area in agriculture and (*right*) forest area over the 1960–2009 period. The regional estimates are based on totals for countries listed above (Table 3.1.2), using data from the World Bank online database (World Bank, 2011).

3.2 Global Climate Change and Large-scale Threats

Corals have evolved during the last 240 million years under a naturally varying climate. Recent climate changes resulting primarily from anthropogenic greenhouse gas emissions likely are the most abrupt since the corals first evolved. The recent anthropogenic changes, both global and broadly distributed local impacts, have been referred to as a new geological era, the “Anthropocene” (Crutzen, 2002; Zalasiewicz et al., 2008; Zalasiewicz et al., 2010), and the associated biodiversity changes have been predicted to be the sixth global mass extinction event (Thomas et al., 2004a). The BRT’s concern in evaluating the effects of climate change on coral reefs generally and on the 82 candidate coral species, in particular, is the rapid increase in atmospheric concentrations of greenhouse gases that in turn are increasing the radiative forcing of the global climate system (IPCC, 2007d) and altering ocean carbonate chemistry (ocean acidification).

The Fourth Assessment Report (AR4) of the Intergovernmental Panel on Climate Change (IPCC) determined the following factors of key importance to corals and coral reefs (IPCC, 2007b):

- Atmospheric CO₂ has increased rapidly from its preindustrial level of 280 ppm to over 390 ppm.
- The earth’s system has already warmed, on average, close to 0.74°C globally over the last century.
- This warming is unusual in at least the last 1300 years.
- Most of that warming is the result of anthropogenic causes, primarily greenhouse gas emissions.
- Greenhouse gas emissions are expected to continue increasing.
- Warming is likely to accelerate.
- The planet is already committed to at least another 1.0°C of global warming from past emissions.
- Globally-averaged temperatures are expected to rise at least 0.2°C per decade for the next few decades with the rise in the latter half of the century to be determined by societal actions (or lack thereof) to control CO₂ emissions.
- At our current emission levels, the earth’s climate is expected to warm 4°C (likely range 2.4°C–6.4°C) by the end of this century.
- In addition to the warming trend, other changes are anticipated, including more variable and extreme temperatures and precipitation and changes in wind and storm patterns and ocean circulation.
- Carbon dioxide (CO₂) increases have not only warmed the climate system but also are changing ocean chemistry (acidification).

The analyses and synthesis of information developed for the IPCC AR4 (IPCC, 2007b) are the most thoroughly documented and reviewed assessments of future climate ever issued and represent the best available scientific information on potential future changes in the earth’s climate system. As with any projections of the future, the IPCC AR4 predictions have their limitations. The IPCC used a range of future greenhouse gas emissions scenarios (SRES) (Nakićenović et al., 2000) to develop general, circulation model-based projections of future climate under clearly stated assumptions about socioeconomic factors that will influence greenhouse gas emissions. While variability was found among the different climate models and even greater variability was introduced by the various greenhouse gas scenarios, emission rates in recent years have met or exceeded levels found in the worst-case scenarios, the A2 and fossil fuel intensive A1FI scenarios. As discussed in subsequent sections of this chapter, warming-induced coral bleaching and disease have already resulted in dramatic declines in many coral species on coral reefs around the world.

The IPCC Fourth Assessment Working Group I Report (IPCC, 2007b) provided projections on many of the environmental variables considered in this Status Review Report. These included ocean and atmospheric warming, changes in ocean stratification and circulation, sea-level rise, ocean acidification, and tropical storm frequency and intensity. Additionally, Working Group 2 (IPCC, 2007c) addressed some of the effects of these physical and chemical projections on corals and coral reefs, including bleaching, disease, and changes in calcification. Anthropogenic CO₂ has a long residence time in the atmosphere and is only slowly removed by ocean absorption and other processes. The IPCC AR4 climate models projected out warming of the atmosphere and oceans to year 2100, with the projections largely being dependent on CO₂ emission scenarios that are largely determined by human behavior—the part of the system that imparts the greatest uncertainty in the IPCC scenarios. Ocean warming and changes in other physical and chemical parameters, such as storms, sea level, and acidification, between now and 2050 are largely driven by greenhouse gases that have already been emitted. Accordingly, much less variability is found among models and scenarios during that time frame than the 2050–2100 period. From 2050 to 2100 the results of the AR4 model projections diverge. However, the variability is not primarily driven by differences among models. There is a larger variation among the various IPCC

emission scenarios (representing human behavior options) than among the climate model projections for each scenario. In recent years humans appear to be following the path that results in the highest levels of emissions considered during the AR4.

The IPCC AR4 summarized the differences in certainty between the first and second halves of this century (Meehl et al., 2007): “There is close agreement of globally-averaged surface air temperature (SAT) multi-model mean warming for the early 21st century for concentrations derived from the three non-mitigated IPCC *Special Report on Emission Scenarios* (SRES: B1, A1B and A2) scenarios (including only anthropogenic forcing). . . this warming rate is affected little by different scenario assumptions or different model sensitivities, and is consistent with that observed for the past few decades. . . Possible future variations in natural forcing (e.g., a large volcanic eruption) could change those values somewhat, but about half of the early 21st century warming is committed in the sense that it would occur even if atmospheric concentrations were held fixed at year 2000 values. By mid-century (2046–2065), the choice of scenario becomes more important for the magnitude of multi-model globally-averaged surface air temperature warming. . . About a third of that warming is projected to be due to climate change that is already committed. By late century (2090–2099), differences between scenarios are large, and only about 20% of that warming arises from climate change that is already committed.”

While these projections are cause for substantial concern about the condition of corals in the future, the BRT was most strongly influenced by observations that corals have been bleaching and dying under ocean warming that has already occurred. Additionally, the earth is already “committed” to warming that is expected to exceed 1.0°C in globally averaged temperature (IPCC, 2007b) and more than 0.5°C in most ocean waters around coral reefs (Donner, 2009) (see Section 3.2.2 for details). Given such increases, temperatures are likely to exceed the tolerances for many corals. Unfortunately for corals, there are no indications that major reductions in greenhouse gas emissions will occur in the near to mid-term future (decades) through national or international policies or major changes in the global fossil fuel economy. Thus the AR4 SRES worst-case IPCC CO₂ emissions scenarios will most likely occur (see Section 3.2.1). With this in mind, the IPCC has established new emission pathways for the upcoming fifth assessment report that include a scenario with much higher emissions than those used in AR4 (Gaffney, 2010; Moss et al., 2010).

The BRT determined that ocean warming and related impacts of climate change have already created a clear and present threat to many corals, that this will continue in the future, and that this could be assessed with sufficient certainty out to 2100. Therefore, the threat posed by the most optimistic scenarios of emissions in the 21st century and even the threat posed by committed warming and other climatic changes represent a plausible extinction risk to the 82 candidate coral species. Even worse for corals, ample evidence indicates that emissions will follow a trajectory that will have major consequences for corals. The following section describes the major global changes and impacts considered to pose a potential risk to the 82 candidate coral species. The degree of risk varies among species and regions; this variation is considered in the individual species assessments (Chapters 6 and 7).

3.2.1 Atmospheric CO₂ and emissions trends

The atmospheric concentration of the dominant greenhouse gas, CO₂, has steadily increased from ~ 280 ppm at the start of the Industrial Revolution to over 390 ppm by 2009 (WDCGG, 2010; Figs. 3.2.1, 3.2.2)—the highest concentration of the last 800,000 years (Luthi et al., 2008; Fig. 3.2.2; Petit et al., 1999) and probably the last 20 million years (Pearson and Palmer, 2000). Rates of human-induced CO₂ emissions are also accelerating, rising from 1.5 ppm per year during 1990–1999 to 2.0 ppm per year during 2000–2007 (Canadell et al., 2007; Raupach et al., 2007). These rising emissions have been most strongly driven by global income growth and global population growth (IPCC, 2007a) and exceed rates seen during the past 720,000 years, including during glacial-interglacial transitions (Hoegh-Guldberg et al., 2007; Luthi et al., 2008). While many international, national, and local initiatives have sought to reduce the growth in greenhouse gas emissions, recent emissions growth and an apparent lack of significant international political action to control emissions to date have resulted in an acceleration of CO₂ emissions at or above the worst-case scenario used in the IPCC’s Third and Fourth Assessment Reports (Fig. 3.2.3). These increased emissions have led to and will continue to exacerbate the climate change effects described in the following sections.

The timing of anthropogenic CO₂ enrichment of the atmosphere is especially important as the Earth is already at naturally high CO₂ conditions found during interglacial periods. It is unlikely that the Earth will transition into the next glacial period for quite some time, as that cycle is driven by slow changes in the planet’s orbital characteristics that are strongly reinforced by atmospheric greenhouse gases. While earlier studies indicated that, were it not for anthropogenic greenhouse gases, the atmosphere should already be cooling back toward the next glacial period (Imbrie and Imbrie,

1980), more recent work indicates that orbital forcing alone is sufficient to continue the current interglacial for tens of thousands of years into the future. However, anthropogenic CO₂ is likely to prolong the current interglacial period (Archer and Ganopolski, 2005; Berger and Loutre, 2002), perhaps to 500,000 years (Archer and Ganopolski, 2005). This means that humans are controlling both anthropogenic CO₂ and the climate system to a much greater degree than are changes in orbital forcing.

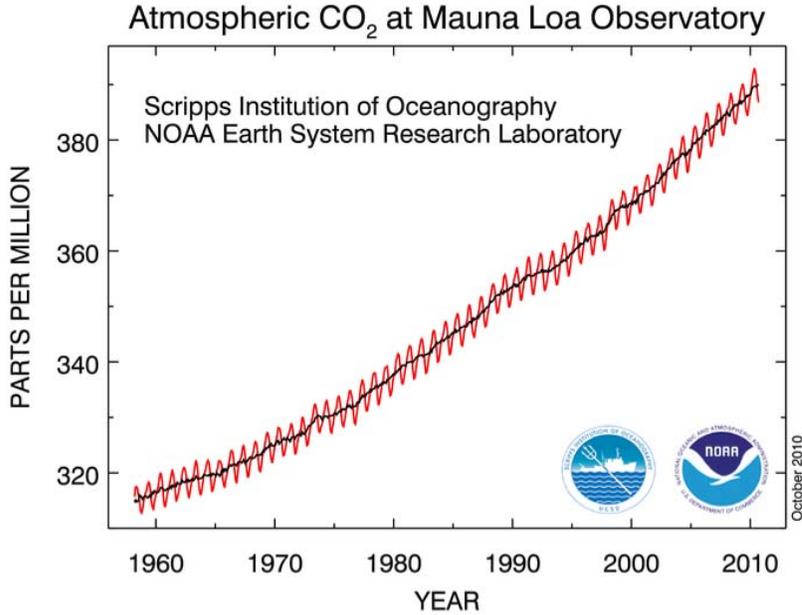


Figure 3.2.1. Time series of atmospheric CO₂, often referred to as the “Keeling Curve”, measured at Mauna Loa Observatory, Hawai’i over the 1958–2010 period (Tans and Keeling, 2010).

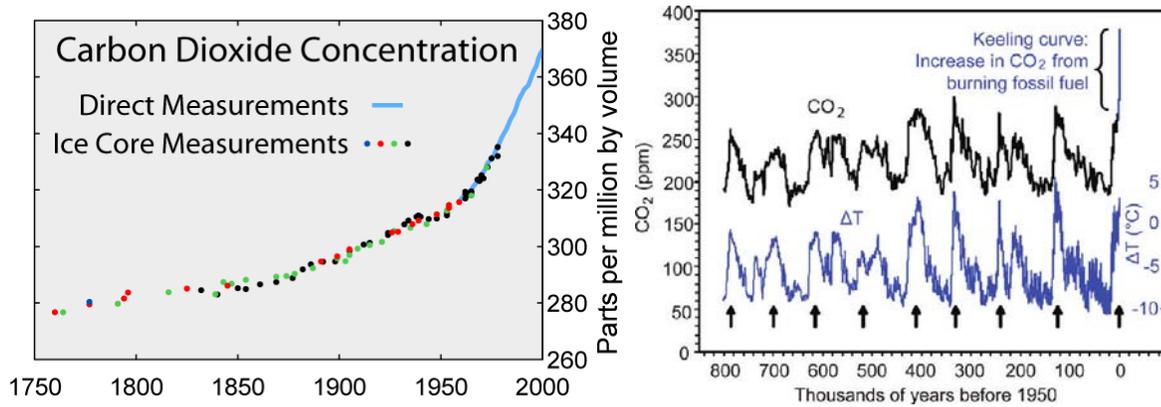


Figure 3.2.2. (Left panel) Global average atmospheric concentrations of carbon dioxide over a 250-year period from 1750 to 2000. The light blue line indicates actual direct atmospheric measurements. The colored dots indicate data gathered from ice cores; each color represents a different ice core sampling site. Data from Robert A. Rohde and the Global Warming Art project. (Right panel) Atmospheric CO₂ and temperature data derived from Antarctic ice core measurements. Arrows mark 100,000-year cycles. Data from Luthi et al., 2008. The “Keeling Curve” (see Fig. 3.2.1) is the vertical segment appended to the ice core data at the upper right.

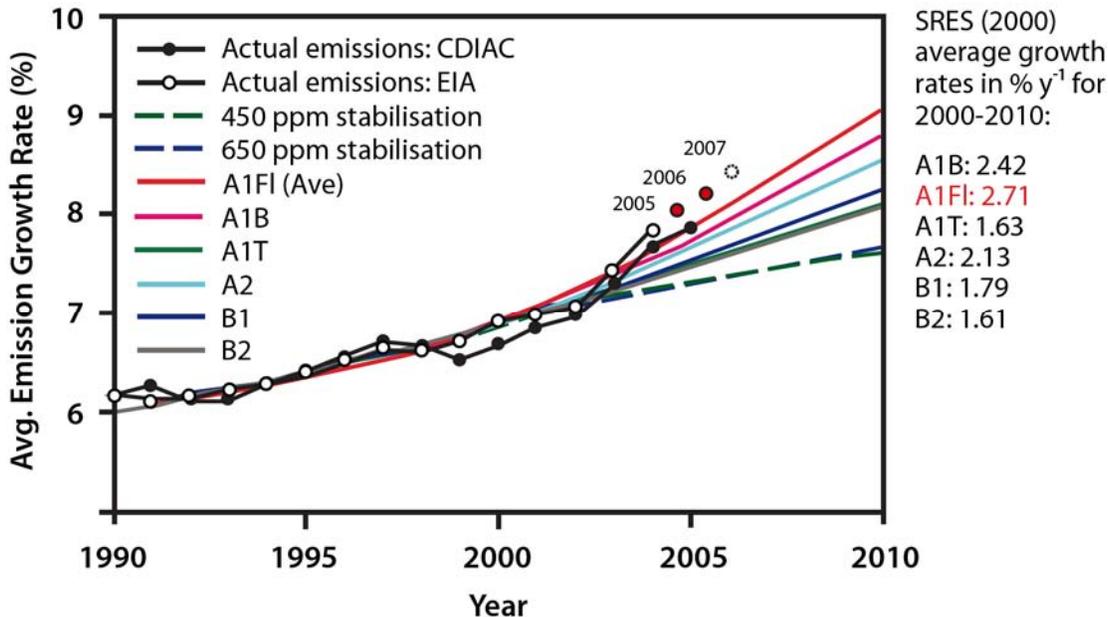


Figure 3.2.3. Observed and projected CO₂ emission growth rates in percent per year (McMullen and Jabbour, 2009; Raupach et al., 2007). The black lines with circles show actual emission rates estimated with two different methods. The solid colored lines show alternative climate model estimates, and the dashed lines show estimates of emission rates required to stabilize CO₂ emissions at a given value. Anthropogenic CO₂ emissions increased by 38% since 1990. The actual emissions growth rate for 2000–2007 exceeded the highest predicted growth rates for the decade 2000–2010 in the emissions scenarios of the IPCC Special Report on Emissions Scenarios (SRES) (Nakićenović et al., 2000). This makes current trends in emissions higher than the worst-case (A1FI) IPCC-SRES scenario.

3.2.2 Ocean warming

It is well documented that the Earth’s temperature has increased during the previous century to levels that had not been reached in over 1,000 years (Chapman and Davis, 2010; IPCC, 2007b). As a result of rising atmospheric greenhouse gases, average global surface air temperatures have already warmed by ~ 0.74°C during the century from 1906 to 2005 (IPCC, 2007b). The rate of warming has also increased from 0.07°C per decade over the past 100 years to 0.13°C per decade for the most recent 50 years (IPCC, 2007b), including increases of up to 0.2°C–0.4°C per decade in waters around many coral reefs (Strong et al., 2008). In particular, the decades of the 1980s and 1990s exhibited a rapid temperature rise to levels above the average for the previous millennium. This average value is the mean of many local measurements, some of which of course are much higher than the average. The global trend in average temperature is reflected in a number of long-term records of sea surface temperature (SST). More important than the global average temperature from a coral perspective, the frequency of warm-season temperature extremes increased during the previous two decades and is inducing more frequent episodes of mass coral bleaching and associated mortality (Eakin et al., 2009).

As rapid as the warming in the previous century has been, the warming in the 21st century is predicted to be greater, even if emissions of anthropogenic greenhouse gases were to cease today (IPCC, 2007b). This “committed” warming is greater than 1.0°C globally averaged temperature (IPCC, 2007b) and greater than 0.5°C in most ocean waters around coral reefs (Table 3.2.1; Donner, 2009). Of course, CO₂ emissions continue to rise, currently at or exceeding the worst-case scenarios used in the IPCC AR4 assessment (Fig. 3.2.3), and the stabilization of atmospheric CO₂ levels is considered unlikely for several decades at least. This worst-case, fossil-fuel-intensive A1FI scenario assumes no substantial changes in emission policies or technologies. At that rate of CO₂ emissions, a further temperature increase in waters around coral reefs of 2.8°C–3.6°C is expected during this century, depending on the ocean basin. At a minimum, ocean temperatures around coral reefs will rise more than 1°C this century, but this would require drastic changes in greenhouse gas emissions across the globe. While significant CO₂ emission reduction would decrease both the ultimate amount and rate of global warming and effects on corals, thus far little movement toward reducing emissions has occurred through international agreements or U.S. legislation. Therefore, reductions are considered unlikely in the short term. Even the most aggressive actions to reduce emissions will only slow ocean warming, not prevent it. Natural

forces put into place by anthropogenic climate change will continue to influence coral reefs for at least 1000 years (Solomon et al., 2009).

Table 3.2.1. Annual mean SST anomaly averaged across each ocean province (from Donner, 2009 Table 1). The columns show global circulation model results of warming to which the Earth is already committed and warming expected from emission scenarios used for the 2001 and 2007 reports of the IPCC (IPCC, 2007b; Nakićenović et al., 2000).

Region	SST anomaly 2030–2039					SST anomaly 2090–2099				
	Commit	B1	A1b	A2	A1f1	Commit	B1	A1b	A2	A1f1
Caribbean	0.4	0.8	0.9	0.9	1.1	0.6	1.5	2.4	2.7	3.4
Middle East	0.4	0.9	1.0	0.9	1.1	0.6	1.6	2.5	3.0	3.5
W Indian	0.4	0.7	0.8	0.8	1.0	0.6	1.4	2.2	2.8	3.4
C Indian	0.4	0.7	0.9	0.8	1.0	0.6	1.4	2.3	2.9	3.5
W Australia	0.3	0.8	0.9	0.8	1.0	0.5	1.3	2.1	2.8	3.4
SE Asia	0.3	0.7	0.8	0.8	0.8	0.5	1.3	2.1	2.7	3.2
GBR+Melanesia	0.4	0.6	0.8	0.8	1.0	0.5	1.2	2.1	2.7	3.3
Micronesia	0.4	0.5	0.8	0.7	1.1	0.5	1.4	2.5	3.0	3.6
Central Pacific	0.4	0.6	0.8	0.7	1.1	0.6	1.4	2.5	3.0	3.6
Polynesia	0.3	0.6	0.6	0.7	0.9	0.4	1.1	1.9	2.3	2.8
East Pacific	0.4	0.8	0.9	0.9	1.1	0.6	1.5	2.4	2.8	3.5
All tropics	0.3	0.6	0.7	0.6	0.8	0.5	1.1	1.8	2.3	2.8

The anomaly for each region is the difference between the projected CM2.0 and CM2.1 ensemble decadal mean SST models and the 1980–2000 ensemble mean
doi:10.1371/journal.pone.0005712.t001

Working Group 2 of the IPCC (IPCC, 2007b) assessed the impact this is likely to have on coral reefs, determining that:

“Corals are vulnerable to thermal stress and have low adaptive capacity. Increases in sea surface temperature of about 1-3°C are projected to result in more frequent coral bleaching events and widespread mortality, unless there is thermal adaptation or acclimatisation by corals.”

In addition, they concluded that ocean acidification would likely reduce coral growth rates, and the likely increase in the intensity of tropical cyclone activity would increase damage from breakage. While there have been a few limited areas where further review has indicated a need to back off from some of the AR4 estimates of future change (e.g., rate of glacier loss in Himalayas) (IPCC, 2010), most research since the IPCC AR4 has shown that, if anything, the 2007 report was optimistic (McMullen and Jabbour, 2009).

A recent independent global analysis of threats to coral reefs (Burke et al., 2011) found that thermal stress, while regionally variable, has indeed influenced corals in all reef regions around the globe (Fig. 3.2.4). Bleaching and mortality of adult coral colonies have been the most visible signs of the effects of climate change, but it is also likely that ocean warming will have detrimental effects on virtually every life history stage of reef corals (Fig. 3.2.5) as impaired fertilization, developmental abnormalities, mortality, and impaired settlement success of larval phases have all been documented (Negri et al., 2007; Polato et al., 2010; Randall and Szmant, 2009a; Randall and Szmant, 2009b).

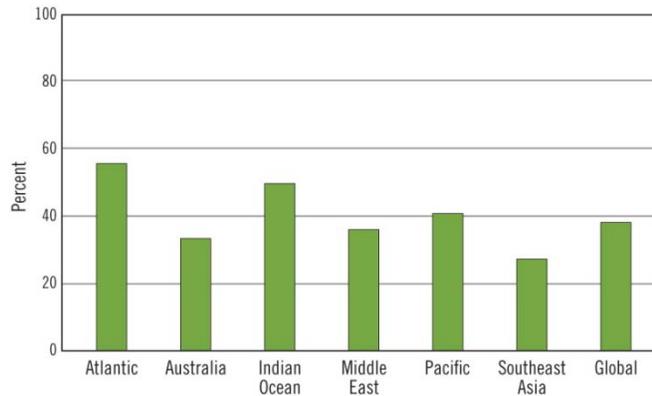


Figure 3.2.4. Global analysis of reef area affected by thermal stress, by region and globally, during the years 1998–2007. Risk was assessed through a GIS-based analysis of risk compiled from NOAA data. For details on methods, please see the original publication. Used with permission from Reefs at Risk Revisited (Burke et al., 2011).

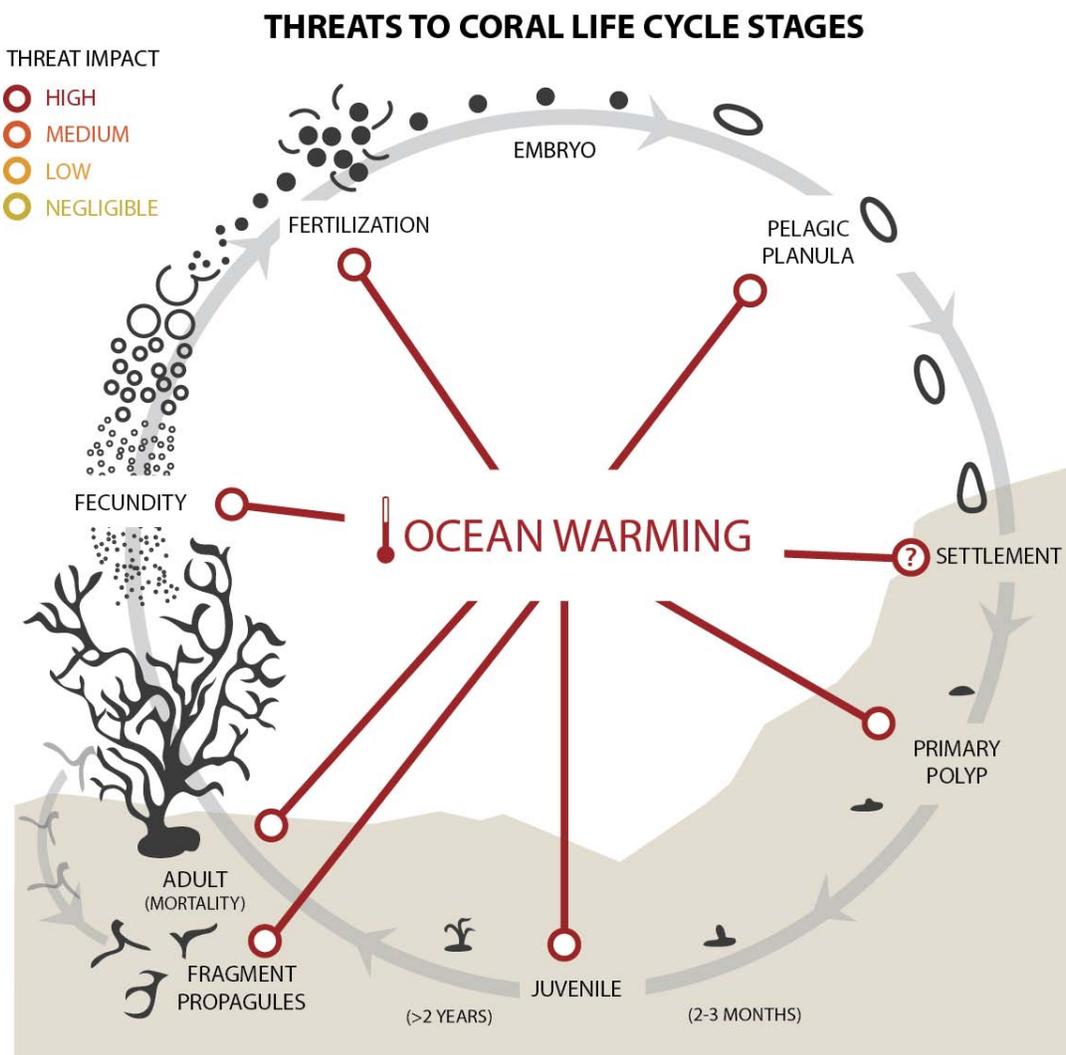


Figure 3.2.5. The impacts of ocean warming on various coral life history stages, including adult mortality, fecundity, and fragmentation, fertilization, pelagic planula, settlement, polyp development, and juvenile growth. Warming ocean temperatures have already had significant effects on corals, leading to the potential extinction of at least one species [see Individual Species Account for *Millepora boschmai* (Appendix) and Glynn et al. (2001)]. The overall contribution of ocean warming to extinction risk for the 82 candidate coral species was determined to be **high** by the BRT. Diagram prepared by Amanda Toperoff, NOAA-PIFSC.

3.2.2.1 Coral bleaching

High temperatures are a significant cause of coral bleaching, the expulsion of the coral's symbiotic zooxanthellae in response to stress. While corals can withstand mild to moderate bleaching, severe, repeated or prolonged bleaching can lead to colony mortality. Many coral physiological processes are optimized to the local long-term seasonal and interannual variations in temperature experienced by the corals, and an increase of only 1°C–2°C above the normal local seasonal maximum can induce bleaching (Fitt and Warner, 1995). Bleaching is best predicted by using an index of accumulated thermal stress above a locally established threshold (Atwood et al., 1992; Eakin et al., 2009). Most coral species are susceptible to bleaching, but this susceptibility varies among taxa (Marshall and Baird, 2000; McClanahan et al., 2007).

While coral bleaching patterns are complex, with several species exhibiting seasonal cycles in symbiotic dinoflagellate density (Fitt et al., 2000), there is general agreement that thermal stress has led to accelerated bleaching and mass mortality during the past 25 years (Brown, 1997a; Eakin et al., 2009). In particular, during the years 1983, 1987, 1995, 1998, and 2005, widespread thermal stress resulting in coral bleaching was documented throughout various parts of the world (Eakin et al., 2009; Eakin et al., 2010; Wilkinson and Souter, 2008; Williams and Bunkley-Williams, 1990). A recent analysis of global-scale thermal stress and reported bleaching events for the 10-year period from 1998 to 2007 (Fig. 3.2.6) shows that this is a widespread threat that has already had significant effects on most coral reefs around the world (Burke et al., 2011). Although some recovery occurred in the Caribbean from the 1987 bleaching event (Fitt et al., 1993) and the 1995 event, the 1998 and 2005 bleaching events resulted in high mortality rates at a number of reefs (Eakin et al., 2010; Goreau et al., 2000; Wilkinson and Souter, 2008). Some areas of the Indian Ocean and Southeast Asia that were showing signs of recovery from a mass bleaching event in 1998 (Wilkinson, 2004) recently experienced another extensive mass bleaching in 2010 (Gillis, 2010).

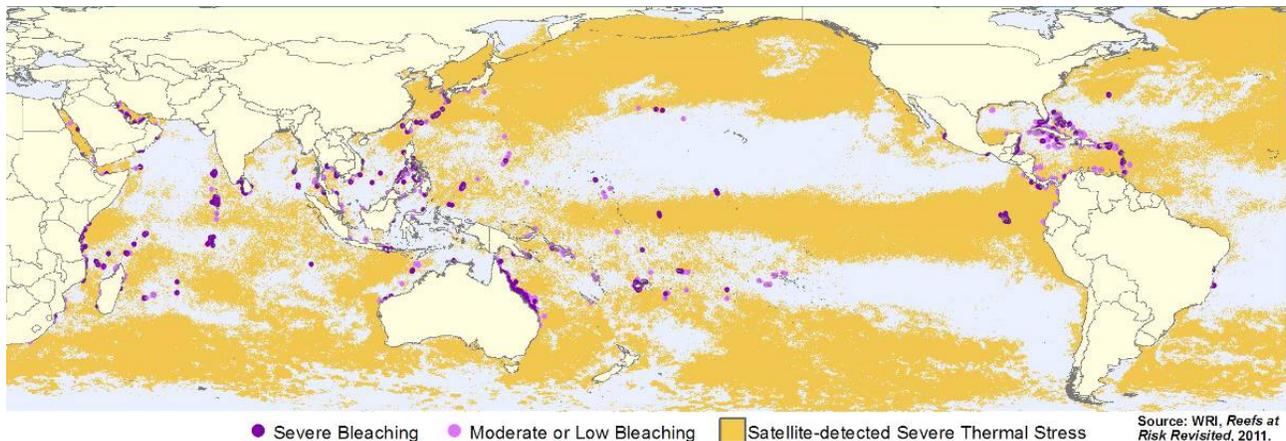


Figure 3.2.6. Global map of reef areas affected by thermal stress during the years 1998–2007. Risk was assessed through a GIS-based analysis of risk compiled from NOAA data. For details on methods, please see the original publication. Source: Reefs at Risk Revisited (Burke et al., 2011).

The repeat of global-scale mass coral bleaching in 2010 demonstrates an important concern about thermal bleaching: at what point do thermal stress events occur too frequently for reefs to have sufficient time to recover? A comparison of the recent and accelerating thermal stress events with the slow recovery rate of most reefs (Baker et al., 2008), suggests that this critical frequency may have already been exceeded. Donner et al. (2005) estimated the adaptation rate that corals must achieve to keep up with anticipated rates of temperature rise this century to be approximately 0.2°C per decade. On most reefs, the rate of warming in the past two decades has exceeded this adaptation threshold (Penaflor et al., 2009; Strong et al., 2008).

Models have provided us with important perspectives on the consequences of future warming on corals. Using global climate models, predictions can be made about the future frequency of thermal events exceeding the bleaching threshold for a given area (Fig. 3.2.7). Hoegh-Guldberg (1999) conducted an early analysis for many regions around the world and predicted that continued ocean warming will result in bleaching episodes as severe as the 1998 event commonly within 15 years and annually in about 40 years. This analysis assumed that the 1998 bleaching did not select for more temperature tolerant genotypes (see below and Baker et al., 2004; Maynard et al., 2008). For many coral species to survive anticipated ocean warming, corals and their zooxanthellae will likely need to undergo significant adaptation

and/or acclimation (Baskett et al., 2009a; Baskett et al., 2009b; Donner, 2009). Two recent modeling studies have also investigated the long-term vulnerability of reefs to mortality resulting from bleaching and other thermal-stress-related disturbances. Models used by Edwards et al. (2010) for the Caribbean and Thompson and Dolman (2010) for the Great Barrier Reef both predict that anticipated levels of bleaching and related mortality are likely to result in significant declines in coral reefs. A recent model study by Hoeke et al. (2011) suggests substantially increased coral mortality and reduced coral growth in the Hawaiian Archipelago over the next 100 years under combined ocean warming and acidification conditions projected using multiple (20) IPCC AR4 models forced by middle-of-the-road CO₂ emission scenarios. Demographic models used by Hernández-Pacheco et al. (2011) predict that bleaching events severe enough to cause mortality are likely to cause continued declines in the population of *Montastraea annularis* if they occur more frequently than once every 17 years (6% probability). This is a troubling statistic for the three species of Caribbean *Montastraea* that are candidates for protection under the U.S. Endangered Species Act as the Caribbean has been hit by six such events since 1985, a return frequency of less than 5 years (Eakin et al., 2010).

Potentially, corals will be able to adapt to rising temperatures. Buddemeier and Fautin (1993) proposed that bleaching may be an adaptive mechanism that allows corals to acquire more thermally tolerant symbionts. The evidence for adaptation was reviewed by Coles and Brown (2003), who determined that previous modeling efforts had not sufficiently taken into account the variability in bleaching response and the potential for adaptation. Baker (2001) found experimental evidence of symbiont switching and documented a rise in the abundance of thermally tolerant symbionts on reefs that recently had bleached (Baker et al., 2004). They concluded that bleaching may lead to reefs that are more resistant to future thermal stress, “resulting in significantly longer extinction times for surviving corals.” Many corals have been found to host multiple lines of dinoflagellate symbionts and may show local variability in the abundance of thermally tolerant symbionts that correspond with local temperatures (Oliver and Palumbi, 2010). Unfortunately, longer-term studies of corals after bleaching have indicated that such symbiont switching may be transient (LaJeunesse et al., 2009; Thornhill et al., 2006). Even where such switches persist, this sort of adaptation is unlikely to impart more than a 1.5°C change in bleaching thresholds (Baskett et al., 2009a). Thus, corals are unlikely to adapt sufficiently to prevent further widespread bleaching or mortality. However, even 1.5°C of adaptation provides some capacity for sustaining reefs in the face of warming likely to exceed 2°C during the 21st century (Donner, 2009). Using the Coral Mortality and Bleaching Model (COMBO), Hoeke et al. (2011) included simulations where the coral heat stress mortality threshold was allowed to “adapt” at a rate of 1.0°C per century (0.1°C per decade). Their results suggested that even with that level of adaptation, modeled Hawaiian corals still suffered extensive mortality from the combined effects of ocean warming and acidification over the next 100 years. Some coral species may adapt sufficiently to avoid extinction during this period, but this is speculative. In addition to adaptation, it is also possible that the geographical range of corals will change in response to increased temperatures (see Section 3.2.2.4). However, in many cases corals will not be able to adapt to acute events as demonstrated by the potential extinction of at least one species [see Individual Species Assessment for *Millepora boschmai* (Appendix) and Glynn et al. (2001)].

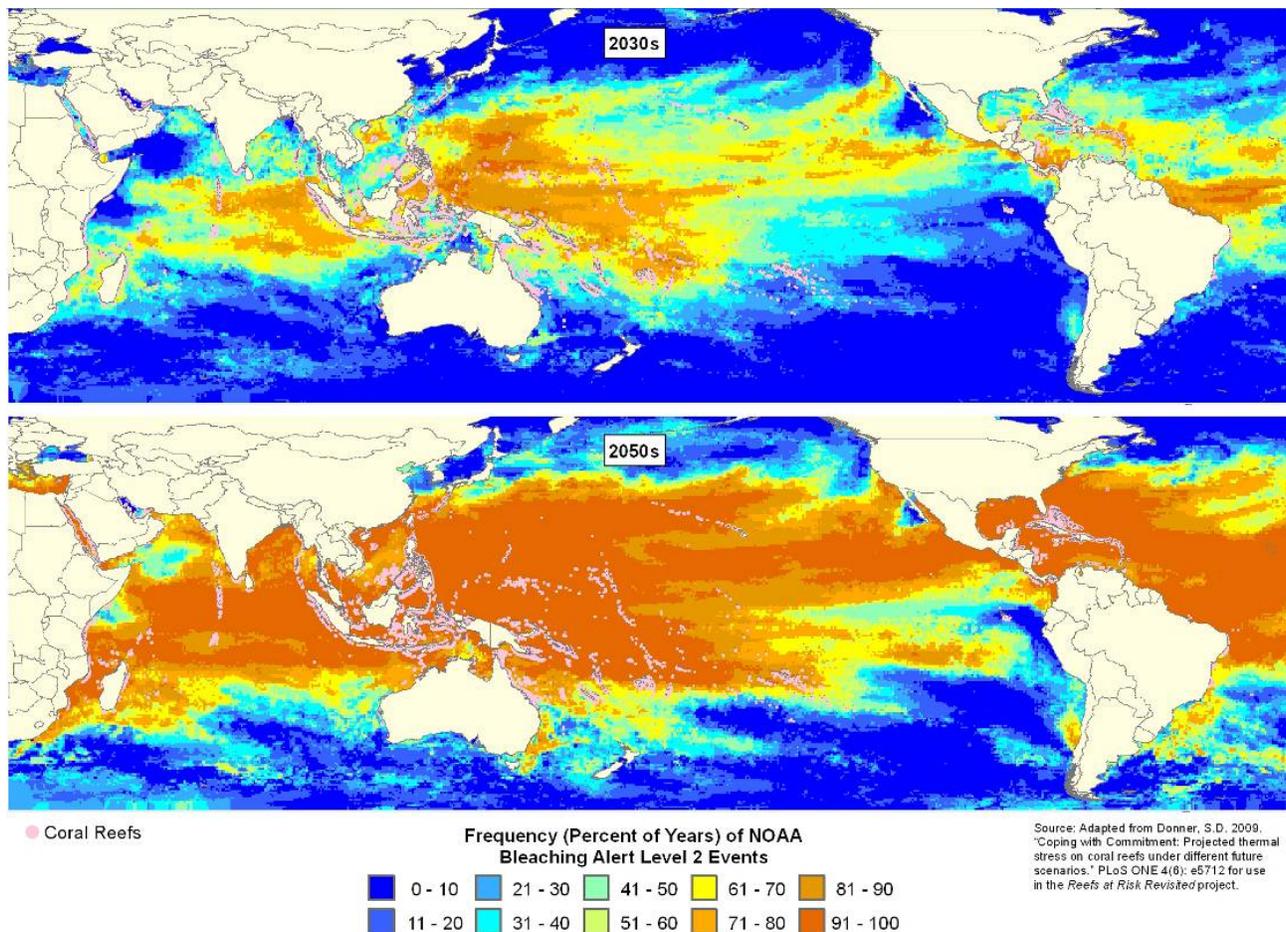


Figure 3.2.7. Global map of reef areas expected to suffer coral bleaching from thermal stress during the decades of the 2030s and 2050s. Risk was assessed through a GIS-based analysis of risk compiled from model data using the IPCC A1B “business as usual” scenario. For details on methods, please see the original publication. Source: Reefs at Risk Revisited (Burke et al., 2011) adapted from Donner (Donner, 2009).

As noted above, corals and reefs can potentially recover from bleaching (Baker et al., 2008), if given sufficient time. Zooxanthellae populations can recover from remnant populations in the coral host or through the acquisition of new symbionts (although new acquisitions are not always stable; Coffroth et al., 2010). Corals that have substantial energy reserves or heterotrophic capacity may be able to withstand the temporary loss of zooxanthellae (Grottoli et al., 2006)—at least, if the corals recover after a couple of months. However, for other corals, loss of zooxanthellae causes starvation, resulting in a significant energy deficit. This translates into less energy available for growth, reproduction, and disease resistance (Baird and Marshall, 2002; Cantin et al., 2010; Ward et al., 2000).

Most of the scientific literature about coral bleaching recognizes temperature as a primary driver of bleaching, but it is also recognized that other factors play important roles. Irradiance, particularly in the ultraviolet (UV) range (Gleason and Wellington, 1993), is perhaps as important as temperature and may be a limiting factor in the dispersal of coral larvae (Wellington and Fitt, 2003). It is important to note, though, that most of the projected increase in UV radiation as a result of ozone depletion will happen well outside the tropics and that only cloud cover changes will likely have a major effect on UV irradiance in the tropics. Because there remains great scientific uncertainty in the parameterizations of water vapor and clouds in current generation climate models, the capability to confidently predict such changes through modeling is minimal. Indications also show that elevated CO₂ (Anthony et al., 2008) can lead to coral bleaching. Microbial infection was observed to cause bleaching in the Mediterranean coral *Oculina patagonica* during warm seasons (Kushmaro et al., 1996; Kushmaro et al., 1997; Rosenberg and Ben-Haim, 2002).

Multiple climate change effects are likely to interact, especially considering the long-term consequences of repeated thermal stress. A recent modeling study predicted that Caribbean coral reefs can maintain their community structure and

function under levels of hurricane damage levels expected this century if other factors remain constant, but anticipated levels of bleaching and related mortality were predicted to cause significant coral reef declines (Edwards et al., 2010). A similar modeling study by Thompson and Dolman (2010) predicted that current rates of recovery were sufficient to compensate for current rates of cyclone and crown-of-thorns seastar damage, but current rates of coral bleaching have resulted in significant declines in acroporid-dominated reefs. Studies have also shown that bleaching thresholds in some species may be influenced by ocean acidification (Anthony et al., 2008) and nutrients (Carilli et al., 2009a; Carilli et al., 2009b; Wooldridge, 2009b; Wooldridge and Done, 2009). It is likely that these stressors are acting in combination to reduce thermal thresholds to bleaching, increase mortality, and slow recovery.

3.2.2.2. *Potential impacts on disease and reproduction*

Increased seawater temperature also may act synergistically with coral diseases to reduce coral health and survivorship (Bruno et al., 2007). Although partially a result of increased surveys to assess disease, observations of the number and severity of coral disease outbreaks over recent decades have shown a significant increase (Harvell et al., 2007). Coral disease outbreaks often have either accompanied or immediately followed bleaching events (Brandt and McManus, 2009; Jones et al., 2004; Lafferty et al., 2004; Miller et al., 2009; Muller et al., 2008). Outbreaks also follow seasonal patterns of high seawater temperatures (Sato et al., 2009; Willis et al., 2004). There are likely many causes of such relationships. To date, these have been identified to include (a) high summer temperatures that increase pathogen virulence or decrease host resistance (Ward et al., 2007) or reduce the antibiotic activity of the host coral's microbial flora (Ritchie, 2006), and (b) the potential of interactions of both winter and summer temperatures on these processes (Heron et al., 2010). The latter is especially important as analyses of global warming patterns indicate that low temperatures during winter months are increasing more rapidly than high temperatures during summer months (IPCC, 2007c). Investigation of potential links comparing temperature anomalies and trends with coral disease has enhanced our understanding of the impacts of ocean warming on coral reefs, particularly when coupled with the observed and predicted increases in the frequency of coral bleaching episodes.

In addition to coral bleaching, mounting evidence suggests that warming temperatures can have direct impacts on early life stages of corals. Studies have shown detrimental effects of anomalously warm temperatures on early life stages of *Acropora millepora* with abnormal embryonic development at 32°C and complete fertilization failure at 34°C (Negri and Heyward, 2000). Fertilization for four other Pacific coral species was less sensitive in this study. In addition to abnormal embryonic development (Lundgren and Hillis-Starr, 2008; Miller, 2002; Polato et al., 2010; Randall and Szmant, 2009a), larval survivorship and settlement success have been shown to be impaired in Caribbean brooding (Randall and Szmant, 2009b) and broadcasting (Lundgren and Hillis-Starr, 2008; Randall and Szmant, 2009a; Voolstra et al., 2009) coral species at temperatures as low as 30°C–32°C. Lastly, the rate of larval development for spawning species is appreciably accelerated at warmer temperatures (Polato et al., 2010; Randall and Szmant, 2009a), which suggests that total dispersal distances could also be reduced, further decreasing the likelihood of potential replenishment of extirpated areas. Similarly accelerated development may occur after corals settle, leading to more rapid growth of coral recruits (Coles, 1985).

3.2.2.3. *Changes to water column stratification (less mixing, less nutrients)*

As warmer water is less dense, ocean warming is and will continue causing increased stratification of the upper ocean. This increased stratification results in decreased vertical mixing of both heat (warmer water down and cooler water up) and nutrients, leaving surface waters warmer and less nutrient-enriched (Behrenfeld et al., 2006). Satellite observations of ocean color have been used to demonstrate decreases in tropical and mid-latitude ocean productivity that correspond with warming and stratification (Behrenfeld et al., 2006; Doney, 2006; Fig. 3.2.8). Polovina et al. (2008) showed that since 1998 the least productive oceanic habitats, the oligotrophic gyres in four of the world's major oceans (North Pacific, South Pacific, North Atlantic, and South Atlantic), have been expanding at average rates between 0.8% per year and 4.3% per year. While the implications for corals and coral reefs of increases in warming-induced stratification have not yet been well studied, it is likely that these changes will both exacerbate the temperature effects described above (e.g., increase bleaching and decrease recovery) and decrease the overall net productivity of coral reef ecosystems (e.g., fewer nutrients) throughout the tropics and subtropics. As one indication of the potential impacts to corals of increased upper ocean stratification, the Hoeke et al. (2011) model simulations for corals in the Hawaiian Archipelago over the next 100 years suggested that even the small differences in temperature (< 0.2°C) between the surface and a depth of 20 m substantially would reduce the rate of heat stress-induced coral mortality for deeper corals (Fig. 3.2.9).

Tropical and mid-latitudes

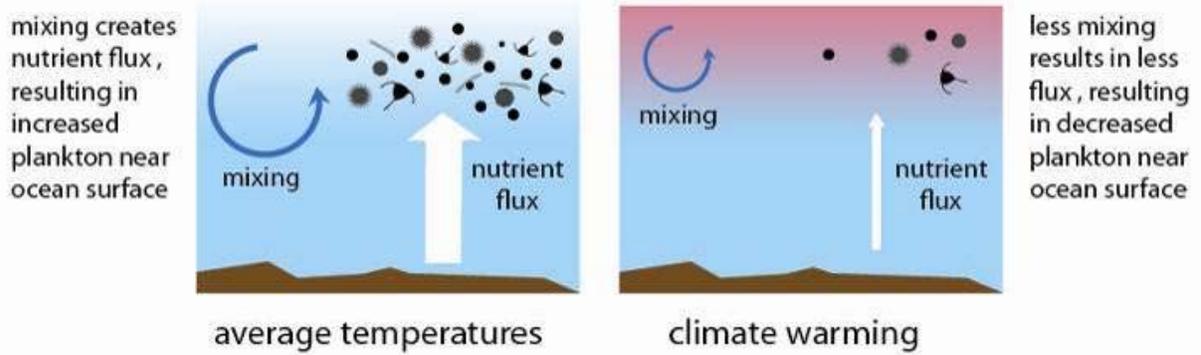


Figure 3.2.8. Predicted phytoplankton response to increased temperature in ocean surface waters in the tropics and mid-latitudes. Phytoplankton are typically nutrient-limited, and satellite data tie reduced biological productivity to upper-ocean warming, reduced stratification, and reduced nutrient supply. Adapted from Doney (2006) by Amanda Toperoff, NOAA PIFSC.

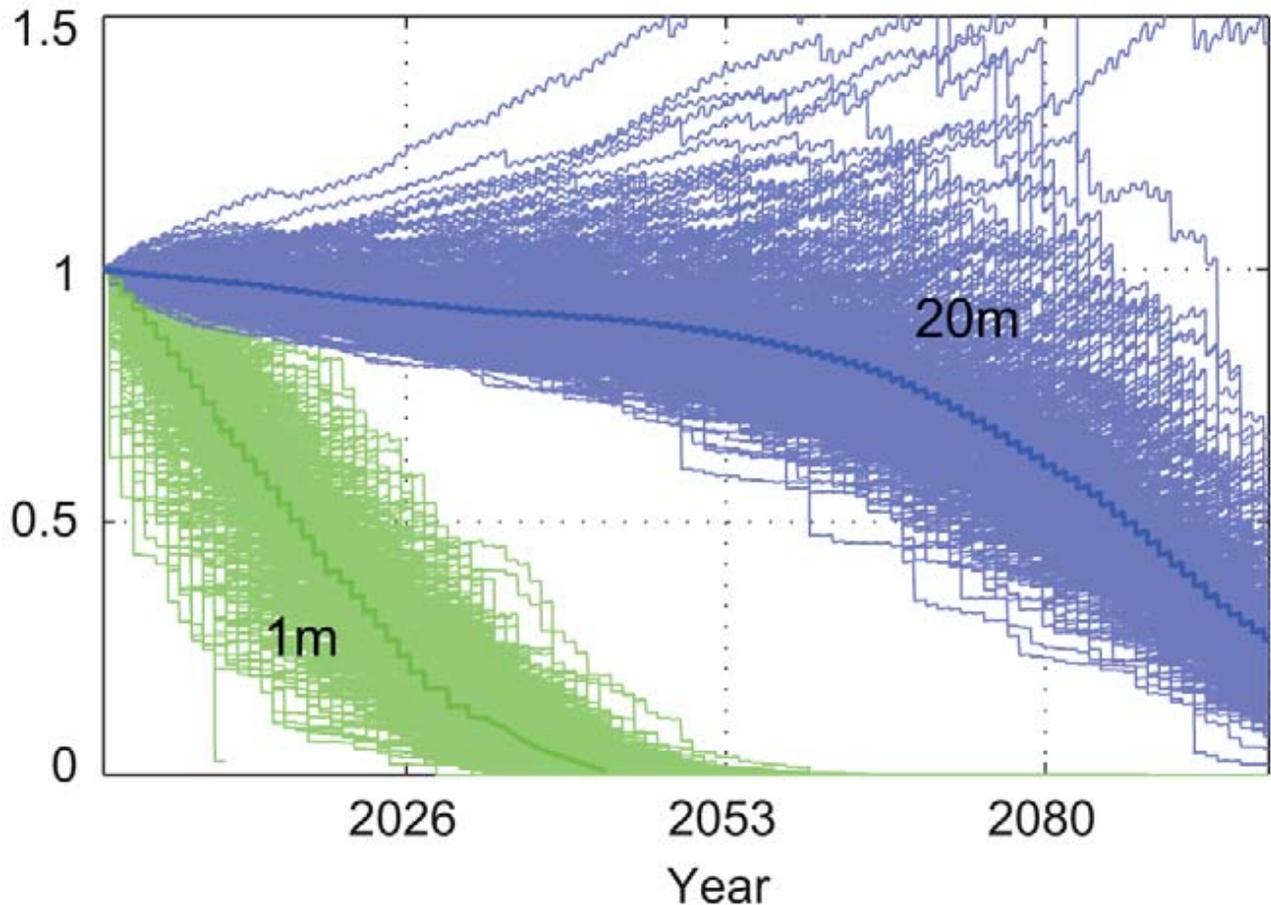


Figure 3.2.9. Monte Carlo projections of fractional change in coral cover assuming in situ temperatures from 1 m and 20 m depths at Pearl and Hermes Atoll in the Northwestern Hawaiian Islands over the next 100 years derived from the Coral Mortality and Bleaching Output (COMBO) model (from Hoeke et al., 2011). In this particular simulation, the corals were assumed to have no temperature adaptation to episodic mortality and calcification was assumed to be reduced by 30% from ocean acidification.

3.2.2.4 The potential for range shifts and biogeographic expansion

Rising ocean temperatures also bring a potential opportunity for range expansion or biogeographic redistributions of many of the candidate corals. Fossil evidence exists of past expansions and contractions in these species' ranges in the Caribbean (e.g., along southeast Florida coast and Flower Garden Banks; Precht and Aronson, 2004; Precht and Miller, 2007), and Australia (Greenstein and Pandolfi, 2008), which coincide with past climate fluctuations and sea-level stands (Precht et al., 2008; Precht and Aronson, 2004). Clemente et al. (2010) reported the recent discovery of a species of *Millepora* in the Canary Islands, at a latitude 11° north of their previous northernmost limit in the eastern Atlantic Ocean. More recently, Yamano et al. (2011) studied nine species of corals in Japan for which survey records were sufficient to detect possible range extensions. They found that in the past 80 years, four of the nine coral species had significantly (and in some cases, rapidly) expanded their range northward in the Japanese Archipelago with no apparent change in their southern range. These included three species of *Acropora* and *Pavona decussata*, the latter being one of the candidate species. Two of the acroporids extended their northward range as much as 13–14 km within a decade. One other acroporid, as well as species of *Caulastrea*, *Favia*, *Hydnophora*, and *Lithophyllon* did not exhibit range changes. Thus, rising ocean temperatures may be expanding tolerable habitats of some corals poleward. Although poleward expansion offers the possibility for thermal refuge for corals, additional habitat requirements and stressors such as lower carbonate saturation state (see Section 3.2.3) and light availability may limit this potential (Kleypas, 1997; Kleypas et al., 1999b). Any range expansion of individual coral species does not imply that reefs will necessarily follow. Buddemeier et al. (2004) argued that such migrations would likely be impeded because human activities—such as coastal development, fishing, pollution, agriculture, and other impacts—have altered the coastal areas where future reefs might otherwise form.

3.2.3 Ocean acidification

As CO₂ concentration has increased in the atmosphere, a corresponding change has occurred in the partial pressures of CO₂ in the surface ocean, resulting in reduced pH (i.e., acidification) and reduced availability of carbonate ions (Fig. 3.2.9).

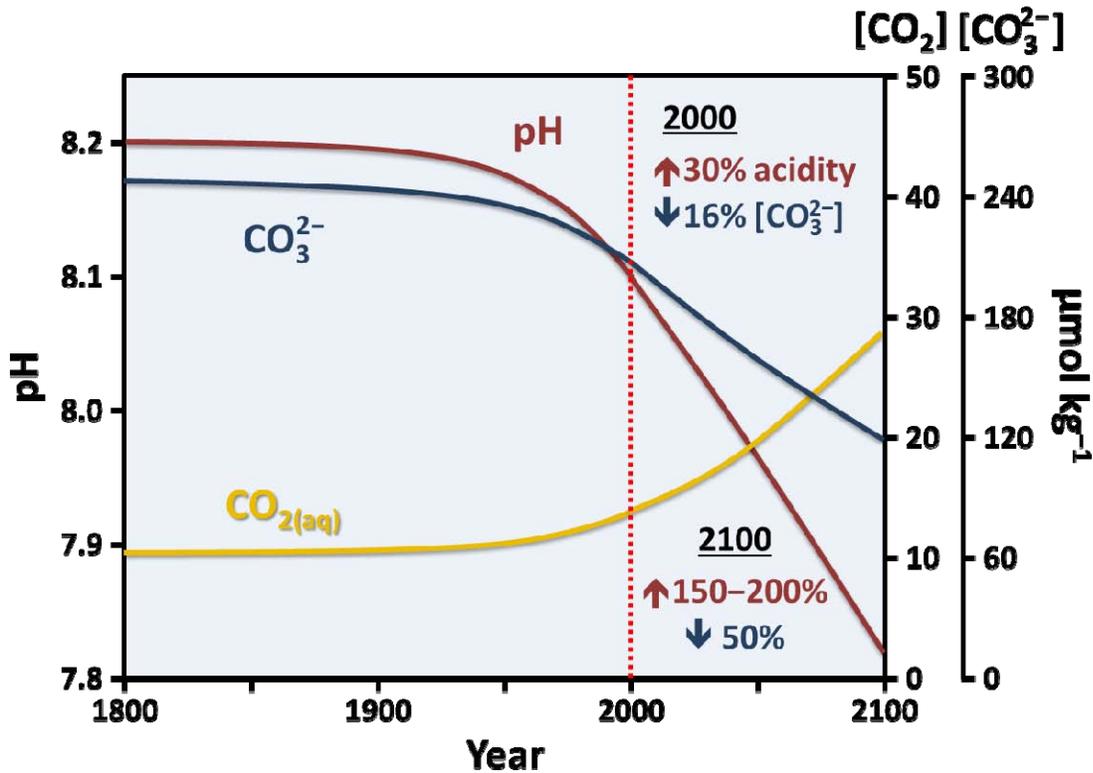


Figure 3.2.10. Projected changes in ocean chemistry as a result of increased atmospheric CO₂ (Wolf-Gladrow et al., 1999).

The dynamics of carbonate chemistry in seawater (shown in Fig. 3.2.10) are frequently summarized by the calcium carbonate saturation state (Ω). At saturation state values less than one, calcium carbonate tends to dissolve into calcium and carbonate ions. At saturation states above about 20, calcium carbonate will spontaneously precipitate (something that naturally happens only occasionally in very few places in the ocean). At saturation states between 1 and 20, organisms can create calcium carbonate shells or skeletons using a physiological calcifying mechanism and the expenditure of energy (Fig. 3.2.11). Different mineralogical forms of calcium carbonate have different solubilities, that is, different saturation states under the same pH conditions. The mineral forms in decreasing order of solubility are amorphous, high magnesium calcite, aragonite, low magnesium calcite. Most coral species, including the candidate species, produce skeletal structures composed of the relatively soluble aragonite that serve as the foundation of coral reefs. Crustose coralline algae, which are also important reef builders that often bind or cement unconsolidated reef components together and provide good settlement habitat for corals, generally produce the even more soluble high magnesium calcite. Many studies have indicated that coral reefs need external seawater saturation states at today's levels or greater to thrive (see Kleypas et al., 2006; Kleypas and Langdon, 2006 for reviews; Royal Society, 2005) and that reductions in saturation state may have already reduced coral calcification and/or reef growth in some locations (see Section 3.2.3.1). It is also generally agreed that rising atmospheric CO_2 has the potential to reduce saturation state enough to slow calcification in most corals (Langdon and Atkinson, 2005) and increase bioerosion, and may even result in the net erosion of coral reefs if saturation states reduce sufficiently (Hoegh-Guldberg et al., 2007). One study concluded that reefs will start dissolving once atmospheric CO_2 reaches the equivalent of a doubling of preindustrial levels (i.e., 560 ppm; Silverman et al., 2009).

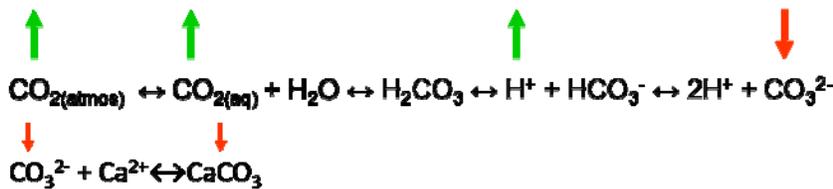


Figure 3.2.11. Seawater carbon chemistry and calcification equilibria. The upper equation shows changes in seawater chemistry from increased atmospheric CO_2 . The system dynamics are such that as atmospheric CO_2 increases, oceanic CO_2 increases, ocean hydrogen ion concentrations increase (lower pH) and carbonate ion concentrations decrease. The lower equation shows the calcification equation (formation of calcium carbonate). As carbonate concentrations decrease, calcification becomes more energetically costly.

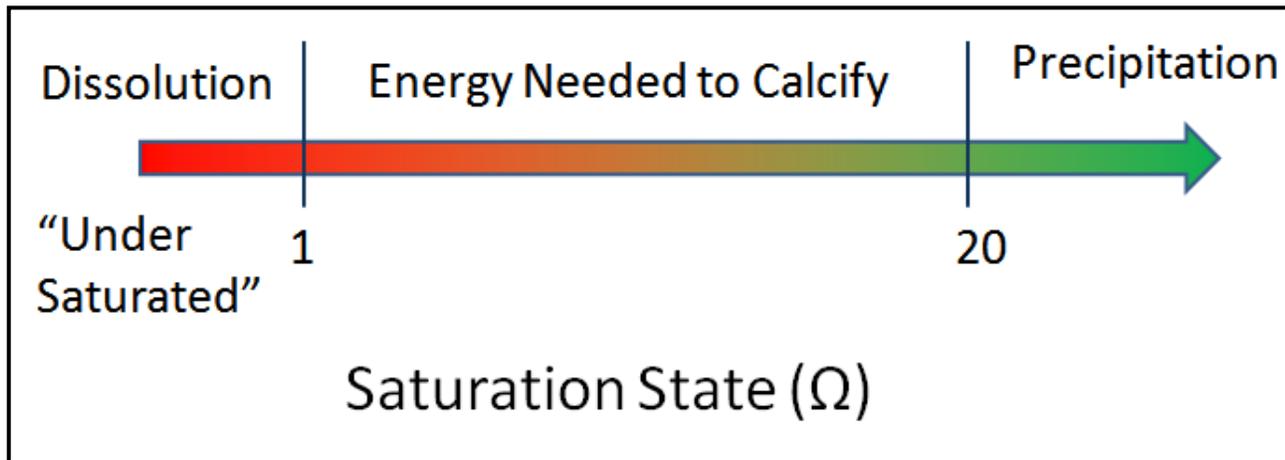


Figure 3.2.12. Relationship between saturation state and the formation of calcium carbonate in seawater.

Although CO_2 levels in the surface waters of the ocean are, on average, generally in equilibrium with the lower atmosphere, there is considerable temporal (Fig. 3.2.12) and spatial variation (Fig. 3.2.13 over a broad range of time (diel to decadal) and space (reef to globe) scales. Five factors generally determine modern oceanic CO_2 levels: (1) the rise in atmospheric CO_2 driven primarily by human activity (see Figs. 3.2.1 and 3.2.12); (2) seasonal variability in atmospheric CO_2 primarily driven by the northern hemisphere seasons (see Fig. 3.2.12); (3) thermodynamic relationships

in CO₂ absorption (i.e., solubility of gases is higher in colder water); (4) local sources of oceanic CO₂ such as upwelling; and, (5) local biological processes of photosynthesis, respiration, and calcification. These factors drive not only changes in surface ocean CO₂ through time, but spatial variability as well. In addition, the aragonite saturation state varies greatly within and across coral reefs and through diel cycles. Much of this variability is driven by photosynthesis, respiration, and calcification by marine organisms. As a result, corals live in an environment that not only is influenced by long, slow changes, but also is highly variable on short time-scales. Additionally, because of biological processes, temperature effects, and ocean circulation patterns, deeper waters tend to have higher CO₂ levels (lower pH) than surface waters.

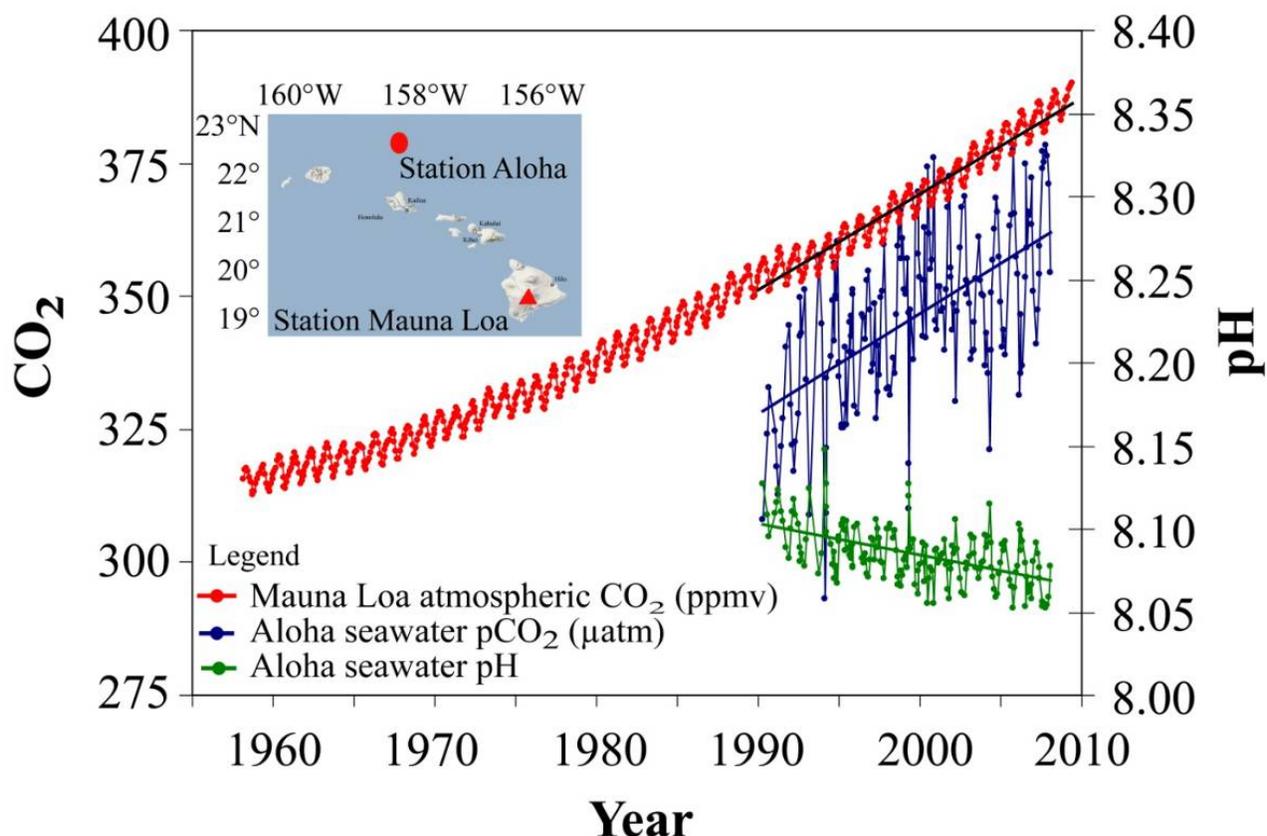


Figure 3.2.13. Time series of atmospheric CO₂ at Mauna Loa (ppmv) and surface ocean pH and pCO₂ (μatm) at Ocean Station Aloha in the subtropical North Pacific Ocean. The station Aloha series has the same slope of increasing CO₂ as seen at Mauna Loa, but the absolute value is lower because of local primary productivity. Figure from Feely et al. 2009 with permission.

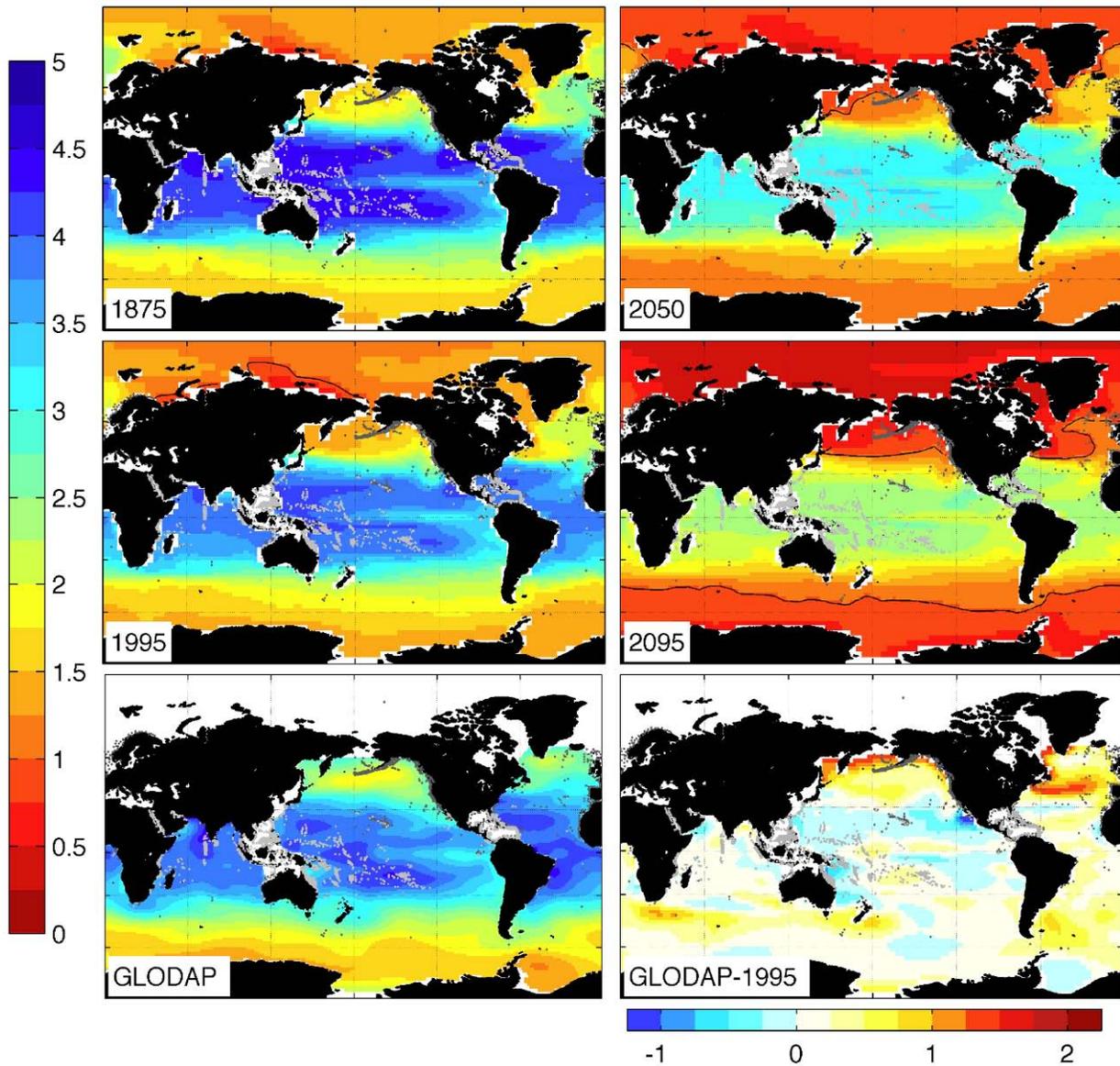


Figure 3.2.14. (Top and middle rows) Model-based decadal mean aragonite saturation state at the sea surface, centered around the years 1875, 1995, 2050, and 2095 (from the National Center for Atmospheric Research Community Climate System Model, version 3 or NCAR CCSM-3). (Bottom left) Global Ocean Data Analysis Project (GLODAP)-based aragonite saturation state at the sea surface, nominally for 1995. (Bottom right) The difference between the GLODAP-based and CCSM-based 1995 fields; note the different color scale of this plot. Deep coral reefs are indicated by darker gray dots; shallow-water coral reefs are indicated with lighter gray dots. White areas indicate regions with no data (Feely et al., 2009).

The changes in ocean carbon chemistry discussed above can substantially reduce coral calcification and reef cementation and may affect many stages of the coral life cycle (Fig. 3.2.14).

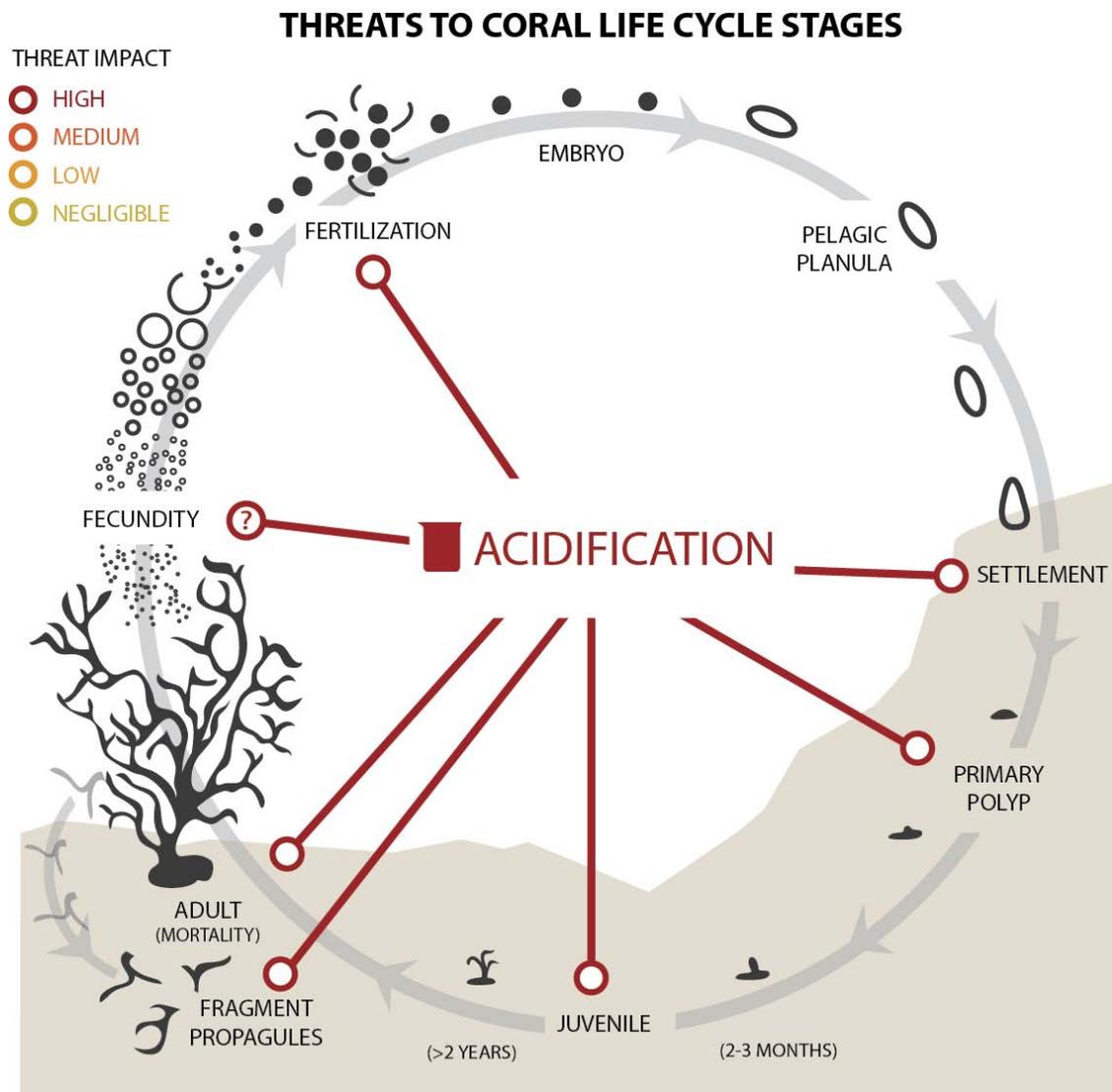


Figure 3.2.15. The impacts of ocean acidification from increasing atmospheric CO₂ to various coral life history stages, including adult growth, fecundity, and fragmentation, fertilization, settlement, polyp development, and juvenile growth. The overall contribution of ocean acidification to extinction risk for the 82 candidate coral species was determined to be **medium-high** by the BRT. Diagram prepared by Amanda Toperoff, NOAA-PIFSC.

3.2.3.1 *Reduced calcification*

Numerous laboratory and mesocosm experiments have shown a relationship between elevated pCO₂ and decreased calcification rates in corals and other CaCO₃ secreting organisms (Barker and Elderfield, 2002; Doney et al., 2009; Table 3.2.2; Riebesell et al., 2000). In an early analysis, Kleypas et al. (1999a) calculated that coral calcification could be reduced by 30% in the tropics by the middle of the 21st century. Subsequent studies continued to show similar results; corals grown during laboratory experiments that doubled atmospheric CO₂ manifested an 11% to 37% reduction in calcification (Gattuso et al., 1999; Langdon et al., 2003; Marubini et al., 2003). A variety of laboratory studies conducted on corals and coral reef organisms (Langdon and Atkinson, 2005) shows that most corals exhibit declining calcification rates (Fig. 3.2.15) with rising pCO₂, declining pH, and declining carbonate saturation state, although the rate and mode of decline can vary among species. Increased pCO₂ slows the laboratory growth rate of *Acropora cervicornis* (Renegar and Riegl, 2005). A study by Schneider and Erez (2006) found that declining saturation state caused a similar reduction in calcification in a Red Sea congener, *Acropora eurystoma*. They showed that *Acropora eurystoma* calcification has already declined by 20% since preindustrial times, and is likely to decline by 35% more with the doubling of atmospheric CO₂ expected by the mid-21st century. These findings are consistent with estimates for

other branching corals (Langdon and Atkinson, 2005) and with atmospheric CO₂ increases in the IPCC AR4 assessment (IPCC, 2007b). However, all experiments do not show declining calcification as saturation state is lowered. Other laboratory studies have shown that even under conditions representing a tripling of preindustrial CO₂ levels (~ 780 ppmv) for 6 months, some corals (*Astrangia poculata*) still calcified normally when provided with sufficient food supplies (Holcomb et al., 2010).

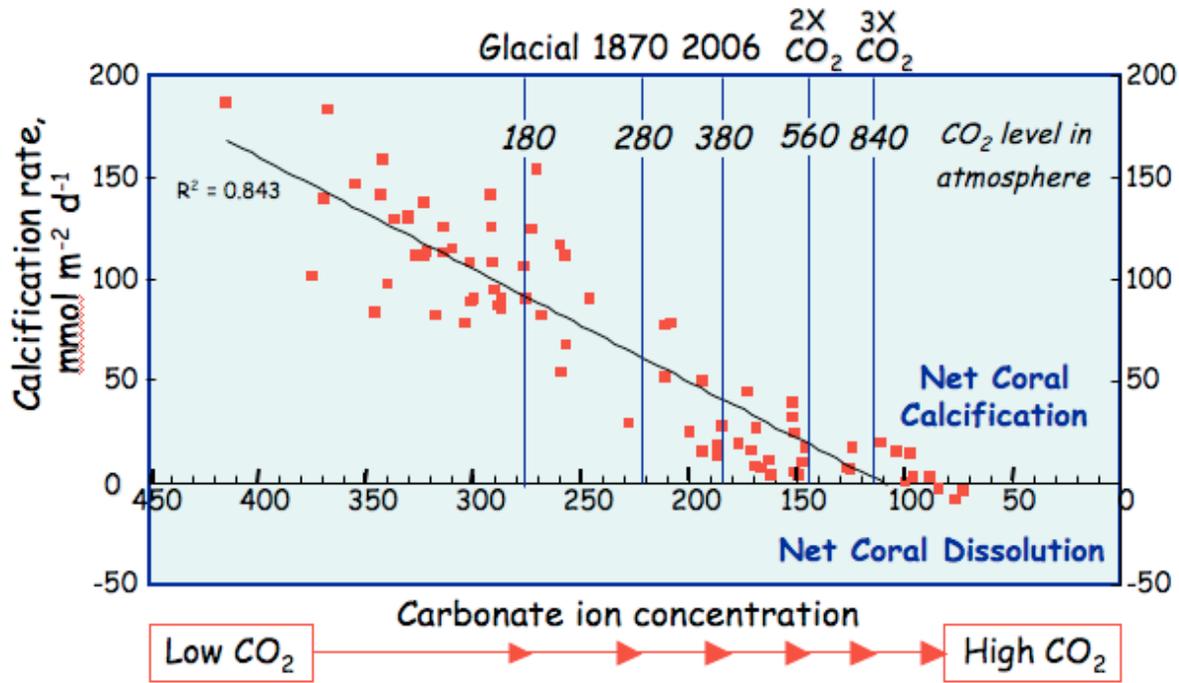


Figure 3.2.16. Plot of calcification rate vs. atmospheric CO₂ expressed as a percentage of the preindustrial rate for a variety of corals and coral reefs during various studies (Langdon and Atkinson, 2005). The regression is a linear model showing declining calcification with increasing atmospheric CO₂. Note: recent studies indicate that responses within a species may be nonlinear (De Putron et al., 2010; Ries et al., 2010).

Such laboratory studies have documented a range of coral responses to ocean acidification, in part because of variations in laboratory manipulations, and in part from processes that may vary in the field. For example, the Holcomb et al. (2010) study found that coral calcification rates were not significantly affected by moderately-elevated nutrients at ambient CO₂ and were negatively affected by elevated CO₂ at ambient nutrient levels. However, the corals reared under both elevated nutrients and elevated CO₂ calcified at rates that did not significantly differ from those of corals reared under ambient conditions. This suggested that elevated CO₂ (reduced saturation state) may only impair the calcification response in corals that are nutrient limited. Under nutrient-enriched conditions, corals may have the ability to use more dissolved inorganic carbon and maintain their calcification rates. This may point out a protection, whereby high nutrient regimes may impart some protection to corals in future acidified seas. Alternatively, the level of acidification tested could account for differences in observed results, as some corals may have what amounts to a threshold response to ocean acidification. For example, the coral *Oculina arbuscula* had minimal changes in skeletal accretion at aragonite saturation states from 2.6 to 1.6, but a major reduction in accretion at a saturation state of 0.8 (Ries et al., 2010).

Table 3.2.2. Summary studies exposing corals to manipulated seawater carbon chemistry (or related treatments). The studies used different methods for carbon manipulation, treatment levels, species response measurement methods and different treatment co-factors (e.g., temperature, nutrients). These differences are important and it is necessary to understand these differences when interpreting this table, which only summarizes a few key findings. Response symbols denote net result of increasing atmospheric CO₂ on organisms, where appropriate. Candidate species are shown in bold.

Species	Response to elevated CO ₂ /lower pH (or other carbon system manipulation as indicated)	Life-Stage Tested	Re-sponse	Source
Caribbean				
<i>Acropora cervicornis</i>	Reduced growth rate	Adult	↓	Renegar and Riegl, 2005
<i>Acropora cervicornis</i>	Switch from aragonite to calcite in simulated Cretaceous seawater	Adult	n/a	Ries et al., 2006
<i>Acropora palmata</i>	Reduced fertilization success, reduced settlement (on treatment-conditioned substrates), reduced post-settlement growth	Recruits	↓	Albright et al., 2010
<i>Porites astreoides</i>	No effect on settlement, negative effect on post settlement skeletal growth	Recruits	-, ↓	Albright et al., 2008
<i>Porites astreoides</i>	Non-linear reduction of calcification by recruits	Recruits	↓	De Putron et al., 2010
<i>Favia fragum</i>	Minor reduction in calcification when fed	?	↓	Cohen and Holcomb, 2009
<i>Favia fragum</i>	Non-linear reduction of calcification by recruits	Recruits	↓	De Putron et al., 2010
<i>Oculina arbuscula</i>	Non-linear reduction in adult skeletal accretion, only “minimally impaired” until below saturation	Adult	↓	Ries et al., 2010
Pacific				
<i>Madracis auretenra</i>	No effect of reduced [carbonate] or lower pH on calcification when [bicarbonate] is kept high	?	?	Al-Moghrabi et al., 1993
<i>Pocillopora damicornis</i>	Still able to recruit	Recruits	-	Jokiel et al., 2008
<i>Stylophora pistillata</i>	Decreased calcification (note: manipulated Ca, not CO ₂)		↓	Gattuso et al., 1998
<i>Stylophora pistillata</i>	Decreased calcification at high temperatures, no effect on calcification at normal temperatures, increased photosynthesis		↓	Reynaud et al., 2003
<i>Acropora digitifera</i>	No effect on larval survivorship, reduced post-settlement growth, slower zoox infection	Larvae	-, ↓	Suwa et al., 2010
<i>Acropora digitifera</i>	Depressed larval metabolism and metamorphosis	Larvae	↓	Nakamura et al., 2011
<i>Acropora eurystoma</i>	Reduced calcification		↓	Schneider and Erez, 2006
<i>Acropora intermedia</i>	Increased bleaching, productivity increase at moderate CO ₂ increase but decrease at highest CO ₂ , slight negative calcification,	Adult	↓	Anthony et al., 2008
<i>Acropora tenuis</i>	Reduced larval survivorship,	Larvae	↓	Suwa et al., 2010
<i>Acropora verweyi</i>	Lower calcification rate, altered crystal structure	Adult	↓	Marubini et al., 2003
<i>Montipora capitata</i>	Decreased calcification and linear extension, no change in gamete production	Adult	↓, -	Jokiel et al., 2008
<i>Montipora digitata</i>	Switch from aragonite to calcite in simulated Cretaceous seawater	Adult	n/a	Ries et al., 2006
<i>Montipora verrucosa (capitata)</i>	Increased net production (in low nutrient), decreased calcification with added HCl	Adult	↓	Langdon and Atkinson, 2005
<i>Astrangia poculata</i>	Nutrient dependent decrease in calcification	Adult	↓	Holcomb et al., 2010
<i>Porites compressa</i>	Increased net production (in low nutrient), decreased calcification with added HCl	Adult	↓	Langdon and Atkinson, 2005
<i>Porites cylindrica</i>	Switch from aragonite to calcite in simulated Cretaceous seawater	Adult	n/a	Ries et al., 2006
<i>Porites lobata</i>	Slight increase in bleaching at highest CO ₂ , decreased productivity with CO ₂ , slight negative calcification effect, interactions with temperature	Adult	↓	Anthony et al., 2008
<i>Porites lutea</i>	Lower calcification rate	Adult	↓	Ohde and Hossain, 2004
<i>Pavona cactus</i>	Lower calcification rate	Adult	↓	Marubini et al., 2003
<i>Galaxea fascicularis</i>	Increased calcification with increased Ca (note: manipulated Ca, not CO ₂)	Adult	n/a	Marshall and Clode, 2002
<i>Galaxea fascicularis</i>	Lower calcification rate	Adult	↓	Marubini et al., 2003
<i>Turbinaria reniformis</i>	Lower calcification rate, altered crystal structure	Adult	↓	Marubini et al., 2003
Other Coral				
Tropical 25 genera of coral	Decreased calcification, no change in community net production	Adult	↓	Langdon et al., 2003
Red Sea coral reef community	Calcification increased with saturation state and temperature	Adult	↓	Silverman et al., 2007
<i>Cladiella</i> sp. (soft coral)	No carbon manipulation but illustrates relationship of tissue	Adult	n/a	Tentori and Allemand,

Species	Response to elevated CO ₂ /lower pH (or other carbon system manipulation as indicated)	Life-Stage Tested	Re-sponse	Source
	damage to calcification			2006
<i>Lophelia pertusa</i> (cold water)	Reduced calcification rate (but still positive net calcification)	Adult	↓	Maier et al., 2009
Non-Coral				
Crustose coralline algae	Negative effect on productivity, net dissolution	Adult	↓	Anthony et al., 2008
Crustose coralline algae	Significant reduction in cover	Recruit and Adult	↓	Jokiel et al., 2008
Crustose coralline algae	Significant reduction in cover	Recruit and Adult	↓	Kuffner et al., 2007
Crustose coralline algae	Decreased calcification/high mortality with temperature	Adult	↓	Martin and Gattuso, 2009

In addition to the variability of results, two aspects of these calcification studies limit the degree to which they could be applied directly to the deliberations of the BRT in evaluating extinction risks. First, most of the 82 candidate coral species have yet to be subjected to acidification studies. This means that the BRT mostly had to rely on work performed on other species in the same genus or family or use the general patterns seen across the few corals that had been tested. Secondly, these laboratory and mesocosm-type experiments have provided only days to months for the corals to acclimatize to the experimental conditions and have used varied techniques (usually addition of acid or dissolved CO₂). However, experiments to date have shown no ability for corals to acclimate or adapt to changes in pH or saturation state, and one of the few experiments to test both acid addition and pCO₂ elevation showed comparable results from both manipulations (De Putron et al., 2010). The response of most corals has been a reduction in calcification, with others being relatively unaffected. Those species that are affected have not shown patterns of acclimatization with the limited exposure times tested to date.

Field studies of the historic growth rates of corals during the last century have also shown variability in results. Recent field studies have shown a decline in linear extension rates in *Porites* spp. from the Great Barrier Reef (De'ath et al., 2009); and Thailand (Tanzil et al., 2009), and of *Acropora palmata* in Curaçao (Bak et al., 2009). Although these studies have suggested that acidification may have already begun significantly reducing growth of some species of coral on some reefs, there is some debate in the community about whether or not the observed reductions in coral growth were indeed caused by acidification. In either case, reductions in coral growth have not been shown for all corals at all reefs, as no effect was seen in *Montastraea faveolata* in Florida (Helmle et al., 2011). This suggests that all corals may not be affected to the same degree or that local factors may be ameliorating the saturation states on reefs. Other studies concluded that some corals are calcifying more, not less, despite changes in atmospheric CO₂ levels (Bessat and Buigues, 2001; Lough and Barnes, 1997). However, the Lough and Barnes (1997) study has largely been superseded by Lough's later work with De'ath (2009). Bessat and Buigues (2001) suggested that corals from Moorea responded positively to small increases in temperature that negated any decrease because of elevated CO₂.

Reduced calcification rates in corals have been hypothesized to manifest in three different possible modes:

1. Corals may grow slower as the reduced aragonite saturation state slows calcification and skeletal extension.
2. Corals may grow at a normal rate, which may reduce skeletal density because the extension rate is faster than the calcification rate. This would result in corals that are more fragile and more easily broken.
3. Corals may divert energy from other processes such as tissue growth or reproduction to maintain calcification rates.

Evidence from numerous studies of calcifying organisms (Langdon and Atkinson, 2005) has suggested that corals affected by reduced saturation state may primarily experience reduced growth (Cohen and Holcomb, 2009), although many uncertainties remain.

While many of the effects of reduced aragonite saturation state have yet to be directly demonstrated in most of the 82 candidate coral species, reduced calcification and slower growth will likely result in slower recovery from breakage, whether natural (hurricanes and storms) or anthropogenic (breakage from vessel groundings, anchors, fishing gear, etc.) or mortality from a variety of disturbances. It also is likely to make it more difficult for corals to keep up with rising sea level. Additionally, slower growth likely implies even higher rates of mortality for newly settled corals that are vulnerable to overgrowth competition, sediment smothering, and incidental predation until they reach a refuge at larger

colony size. Reduced calcification and slower growth suggests it may take more time to reach reproductive size after successful recruitment or fragmentation. Further, ocean acidification is likely to interact with other stressors. Work on Pacific *Acropora* spp. suggests that acidification may reduce the threshold at which bleaching occurs, increasing the threat posed by bleaching (Anthony et al., 2008).

Many other important reef species will be significantly influenced by reduced seawater carbonate saturation state. Recent community mesocosm studies (Jokiel et al., 2008; Kuffner et al., 2007) showed dramatic declines (86%) in the growth rate of crustose coralline algae and other reef organisms (250% decline for rhodoliths) and an increase in the growth of fleshy algae at CO₂ levels expected later this century. The fleshy algae increase presumably occurs because plant species that have an inefficient carbon capturing mechanism can have elevated rates of photosynthesis with increased CO₂. Such decreases in growth of crustose coralline algae, coupled with rapid growth of fleshy algae, would presumably result in less available habitat and more competition for settlement and recruitment of new coral colonies. It has been suggested that these indirect mechanisms (i.e., impacts on reef plants) may account for observed reduced settlement success of coral larvae in elevated CO₂ conditions rather than direct effects of reduced saturation state on metamorphosis/calcification (Albright et al., 2008). Modeling studies have estimated the rates of grazing by herbivores that are required to maintain conditions suitable for coral recruitment and the coral dominance of reef ecosystems (Mumby et al., 2007a). The rates of herbivory necessary to maintain conditions needed for coral recruitment would have to increase as atmospheric CO₂ increases (Hoegh-Guldberg et al., 2007; Fig. 3.2.16).

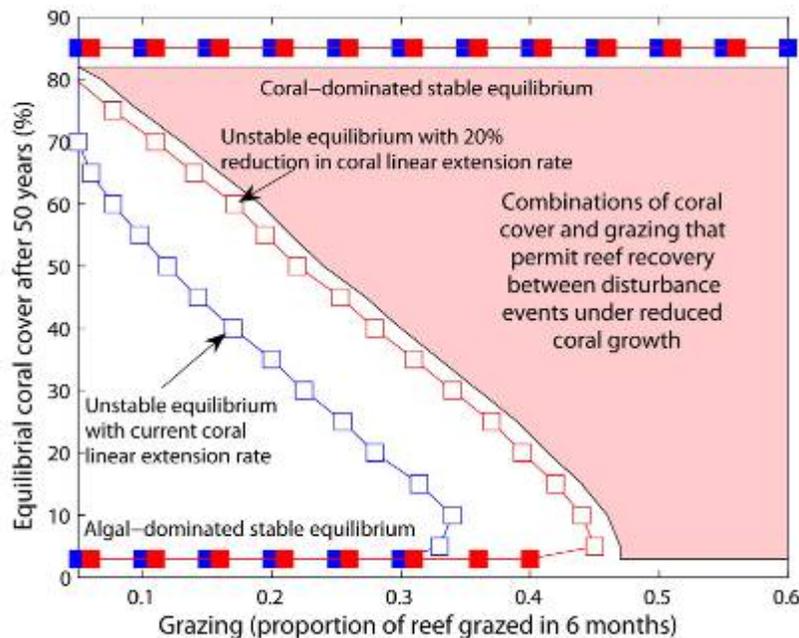


Figure 3.2.17. Model projection of reduction in the resilience of Caribbean forereefs as coral growth rate declines by 20%. Reef recovery is only feasible above or to the right of the unstable equilibria (open squares). The “zone of reef recovery” (pink) is, therefore, more restricted under reduced coral growth rate and reefs require higher levels of grazing to exhibit recovery trajectories (Hoegh-Guldberg et al., 2007, using model from Mumby et al., 2007a; Mumby et al., 2007b).

Additionally, rising atmospheric CO₂ and the resulting reduced carbonate saturation state may reduce the growth rate and recruitment of long-spiny sea urchins (*Diadema antillarum*), thereby deterring recovery of this important keystone species, which declined dramatically during the 1983 mass mortality event in the Caribbean. Ries et al. (2009) found that urchins differ in their response to ocean acidification, with some species decreasing and others having hyperbolic growth responses. Slower recovery of *Diadema antillarum* will keep down grazing rates and increase algal competition for benthic space, especially at sites where the density of other herbivores, such as parrotfishes, have been reduced by fishing. All of this is likely to occur in concert with potential enhancement of growth by some fleshy macroalgae (Kuffner et al., 2007).

3.2.3.2. *Increased erosion*

Another major potential consequence of ocean acidification (falling carbonate saturation state) is a reduction in the structural stability of corals and coral reefs, which result both from increases in bioerosion and decreases in reef cementation. Naturally low saturation states of waters in the eastern Pacific Ocean have resulted in some of the highest rates of bioerosion documented globally (Eakin, 1996; 2001; Glynn, 1988b; Reaka-Kudla et al., 1996) and in poorly cemented (Glynn and Macintyre, 1977; Manzello et al., 2008), unstable, and fragile reef frameworks. These reefs have rapidly crossed the tipping point from net deposition of calcium carbonate framework to net erosion after the severe coral bleaching during the 1983 El Niño warming (Eakin, 1996; 2001; Glynn, 1988b). Low saturation state seawater decreases the rate of the basic biogeochemical processes that create the cements that infill reefs, such as the crustose coralline algae discussed in Section 3.2.3.1 (Jokiel et al., 2008; Kuffner et al., 2007). As atmospheric CO₂ rises globally, new reef formations may calcify more slowly and become more fragile, thereby resembling existing conditions observed for eastern Pacific reefs. This would impede reef growth and decrease the ability of coral reefs to recover from habitat damage resulting from disturbances such as hurricanes, vessel groundings, and anchoring. Many important bioeroders, such as boring sponges, use acidic processes that may be enhanced at lower oceanic pH levels. This may increase biochemical erosion of the reef framework but has yet to be tested. Recent work has shown that topographic complexity has already been reduced in Caribbean coral reefs (Alvarez-Filip et al., 2009), probably as a result of coral mortality and subsequent breakage/erosion of dead skeletons. This topographic flattening reduces shelter habitat for herbivores, thereby further increasing ecosystem impacts. Corals themselves may be able to persist and maintain some level of physiological function in the absence of a carbonate skeleton (Fine and Tchernov, 2007), but a lack of accretion and increased erosion would essentially eliminate coral reefs and much of the ecosystem goods and services they provide. This could begin as early as mid-century when doubling of preindustrial CO₂ concentrations are predicted (Silverman et al., 2009).

Finally, it has been hypothesized that reduced pH and increased dissolved CO₂ may influence coral diseases. However, far too little is known about most coral diseases to estimate this effect, and no studies to date have tested such potential relationships.

3.2.3.3 *Effects on reproduction (fertilization, settlement, recruitment, juvenile growth)*

Despite early work by Edmondson that showed coral larvae can sometimes settle under acidified conditions but vary in their ability to calcify (Edmondson, 1929; 1946), until recently little attention has been directed at the potential effects of ocean acidification on early life stages of corals (Fig. 3.2.14). Ocean acidification can affect non-calcifying stages of organisms through the effects of low pH on their development and physiology (Pörtner et al., 2004). Given the plethora of demographic bottlenecks in the early life stages of corals, the energy-limited state (i.e., lecithotrophic) of most spawned larvae prior to the onset of post-settlement calcification, and the complex, poorly-understood cues that affect larval settlement, it is plausible to expect that basic changes in carbon chemistry may be influential in coral recruitment. Published studies on a few coral species have begun to support these suppositions. More sophisticated manipulations than Edmondson's have shown that post-settlement and juvenile corals show consistent inhibition of calcification and skeletal growth under reduced carbonate saturation state (Albright et al., 2008; Albright et al., 2010; Cohen et al., 2009; Kurihara, 2008; Suwa et al., 2010). Fertilization success of the spawning coral *Acropora palmata* is significantly reduced at increased CO₂ levels projected for within this century. While this impairment was not detectable at optimal sperm concentrations, the relative reduction of fertilization success was greater at the lower sperm concentrations that are more typically realized in nature (Albright et al., 2010). Thus, ocean acidification may exacerbate Allee effects in broadcast spawning corals.

In contrast, some studies now suggest that reduced carbonate saturation state (as low as < 1) has little effect on survivorship during the pelagic larval stage (Suwa et al., 2010). Also, no significant impacts were observed on spawning of *Montipora capitata* and settlement of *Pocillopora damicornis* (brooded) larvae during a 6-month mesocosm experiment with treatment saturation state of 1–2 (Jokiel et al., 2008), although the low number of replicates provided insufficient statistical power to effectively detect potential differences. In contrast, a recent study found that larvae of *Acropora digitifera* responded to reduced pH with reduced metabolism and suppressed metamorphosis, perhaps as a response to increased short-term survival under acute stress (Nakamura et al., 2011). The result of this may reduce long-term larval survival, recruitment, and connectivity under chronically reduced pH.

Effects of low pH on corals may increase again after settlement. Settlement assays conducted with *Porites astreoides* larvae and substrates conditioned at ambient saturation states did not show a significant effect of lowered pH (Albright et al., 2008), while assays with *Acropora palmata* larvae on substrates conditioned in high-CO₂ treatments showed more

than a 50% reduction in settlement success (Albright et al., 2010). This suggests that acidification may influence settlement more by indirect alterations of the benthic community, which provides settlement cues, than by direct physiological disruption. Kuffner et al. (2007) and Jokiel et al. (2008) have both reported the radical reduction in colonization and growth of crustose coralline algae in mesocosm experiments in moderate ocean acidification treatments (ca. 2100 in the IS92a “business-as-usual” emission scenario, IPCC, 1992). This would not only reduce reef accretion and cementation, but it might also reduce the presence of important cues for larval settlement.

3.2.4 Sea-level rise (slow and/or rapid)

3.2.4.1 Sea-level rise—processes and predictions

The IPCC Fourth Assessment Report (AR4) (IPCC, 2007b) concluded that sea level will continue to rise because of thermal expansion and the melting of both land and sea ice as direct consequences of increases in atmospheric greenhouse gases. The most often quoted range for the next century does not include the potentially largest component: the melting and sliding of the Greenland and Antarctic ice sheets. As stated in the summary for policy makers: “Models used to date do not include uncertainties in climate-carbon cycle feedback nor do they include the full effects of changes in ice sheet flow, because a basis in published literature is lacking.” This means that the IPCC projection of a 0.3–0.6 m sea level rise by 2100 (A1FI scenario) should be considered a minimum amount as it omits the potentially largest component of sea-level rise. However, as evidence accrues that suggests that the Greenland and Antarctic ice sheets are much more dynamic and vulnerable than previously thought, more recent studies have increased the estimated rates for sea-level rise (Overpeck et al., 2006; Rahmstorf et al., 2009; Shepherd and Wingham, 2007; Thomas et al., 2004b). It now appears most likely that sea-level rise over the 21st century will be at least 1–2 m (Cabioch et al., 1998; Overpeck and Weiss, 2009), with sea-level rise of 4 m less likely but not out of the question by 2100 (Rahmstorf et al., 2009). The IPCC went on to conclude that an additional 4–6 m rise would be likely if polar land-ice melting is similar to that seen during the last interglacial period, 125,000 years ago, and 7 m is possible if the Greenland ice sheet melts completely. At current rates of anthropogenic greenhouse gas increases, it is not a question of if these sea levels will be reached, but perhaps when (McMullen and Jabbour, 2009; Milne et al., 2009). Sea-level rise has consistently exceeded the worst-case scenario (A1FI) from IPCC estimates (Rahmstorf et al., 2009). The best estimates of the rates of sea-level rise attributed to ice melting and thermal expansion during this century are between 0.8 and 2.0 m (Pfeffer et al., 2008).

3.2.4.2 Impacts to corals and coral reefs

An increase in sea level (or increased depth via subsidence) provides accommodation space for corals living near the sea surface, which corals can potentially fill through vertical growth. However, it is likely to affect multiple stages of a coral’s life history and the BRT ranked it as a low-medium overall threat (Fig. 3.2.17). Depending on the rate and amount of sea-level rise, reefs may be able to keep up or catch up—but rapid rises can lead to reef drowning (Neumann and Macintyre, 1985). Rapid rises in sea level could affect many of the candidate coral species by both submerging them below their common depth range and, more likely, by degrading water quality through coastal erosion and potentially severe sedimentation or enlargement of lagoons and shelf areas. Blanchon and Shaw (1995) argued that a sustained sea-level rise of more than 14 mm per year is likely to displace the very rapidly-growing Caribbean elkhorn coral *Acropora palmata* from its framework-building depth range (0 to 5 m) into its remaining habitat range (5 to 10 m) where a mixed framework is likely to develop. Many corals that inhabit the relatively narrow zone near the ocean surface have rapid growth rates when healthy, which historically has allowed them to keep up with sea-level rise during the past periods of rapid climate change associated with deglaciation and warming (Blanchon et al., 2009; Church et al., 2001; Thomas et al., 2004b). Recent work in the Yucatan region of Mexico by Blanchon et al. (2009) indicated that during the warming that led to the last interglacial period, *Acropora palmata* was able to keep up with the first 3 m of rapid sea-level rise. Continued sea-level rise led to the demise of the original forereef crests, and *Acropora palmata* began to grow again at a more inland site as sea level rose a total of 6 m over 50–100 years. Even at the most rapid trajectories of sea-level rise, it is likely that many of these corals would be capable of keeping up (growing upward) if conditions were otherwise suitable for growth. However, rapid growth is likely to be hindered if the corals are stressed by other factors. In contrast, corals that predominantly inhabit wider depth ranges are less likely to suffer negative effects from sea-level rise—provided that water quality does not seriously deteriorate, which could limit light in the deeper portions of some species’ depth ranges.

Sea-level rise may cause decreased water quality via shoreline erosion and flooding of shallow banks and lagoons. The threat of these processes can be assessed on a site-by-site basis, using criteria such as the geological character of the shoreline and topography. Where topography is low and/or shoreline sediments are easily eroded, corals may be severely stressed by degrading water quality, heavy levels of sedimentation, and potential release of toxic contaminants

as sea-level rise proceeds. Greater inundation of reef flats can erode residual soils and lagoon deposits (Adey et al., 1977; Lighty et al., 1978) and produce greater sediment transport (Hopley and Kinsey, 1988). Flooded shelves and banks may alter the temperature or salinity of seawater to extremes that can then affect corals during offshore flows. This process has been termed reefs that “are shot in the back by their own lagoons” by Neumann and Macintyre (1985). Although this process could be widespread, many coral reefs will have areas, particularly mid-ocean low islands and atolls and windward sides of rocky islands, where erosion and lagoon formation will be minimal. However, Blanchon et al. (2009) showed that ocean warming and sea level rise leading up to the last interglacial period resulted in either smothering and burial of lagoon corals or a transition of coral communities to a more sediment-tolerant assemblage. The new coral communities included slower-growing species most able to withstand sediment backwash during shoreline retreat. Hence, rapid sea-level rise may result in either loss of corals or changes in community structure and composition of corals, most likely to slower growing forms.

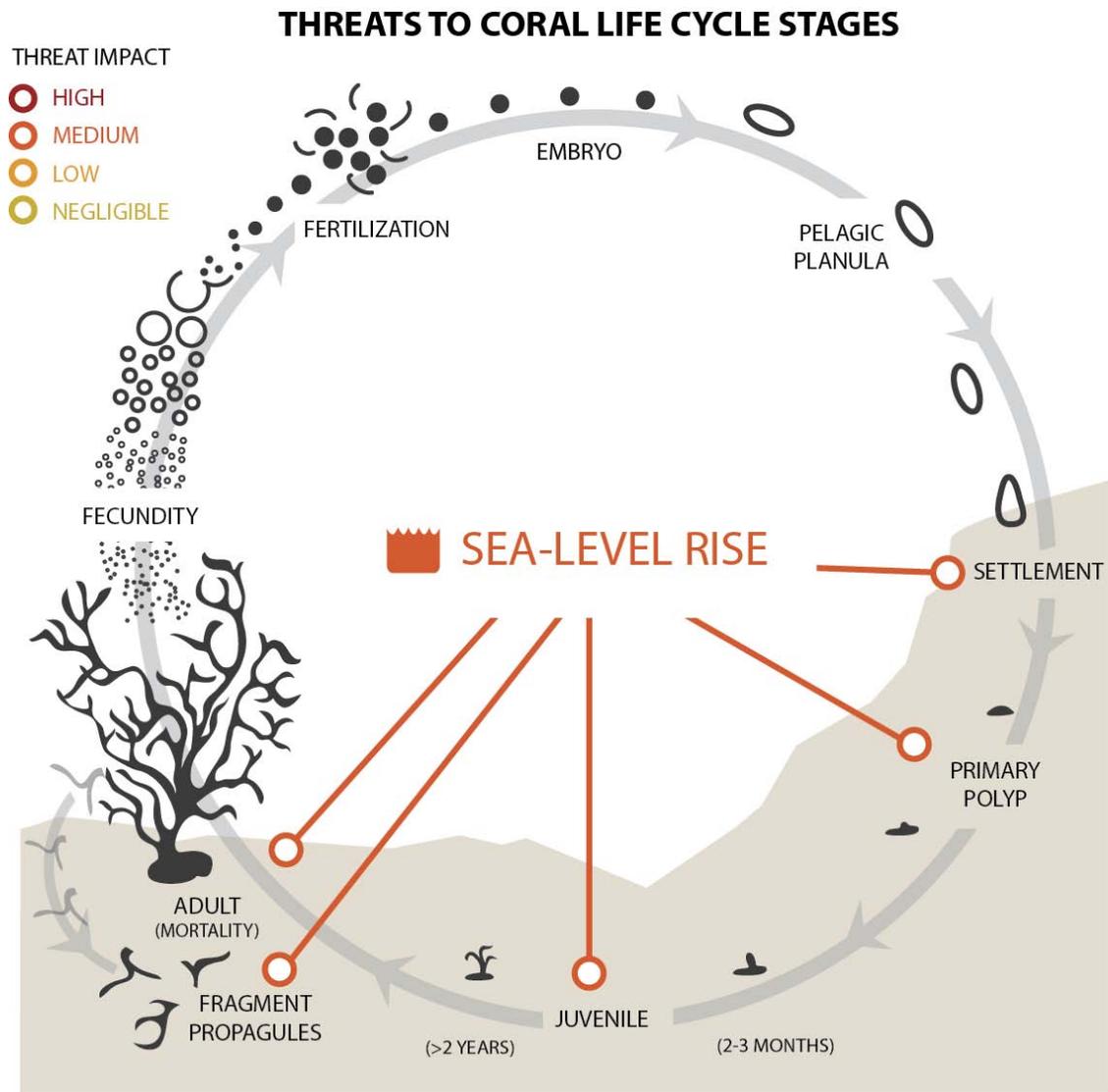


Figure 3.2.18. The impacts of sea-level rise to various coral life history stages, including adult mortality and fragmentation, settlement, polyp development, and juvenile growth, mostly as a result of increased sedimentation and decreased water quality (reduced light availability) from coastal inundation. The overall contribution of sea-level rise to the extinction risk of the 82 candidate coral species was determined to be **low-medium** by the BRT. Diagram prepared by Amanda Toperoff, NOAA PIFSC.

Previously, coral reefs have responded to post-glacial sea-level rise with rapid growth followed by reef retreat to follow shoreline retreat. This requires that corals have access to unobstructed framework that will serve as the substrate for new reef growth. In many areas, human response to rapid sea-level rise is likely to result in “hardening”—coastal construction designed to protect critical human infrastructure from advances of the sea into coastal communities. Under such scenarios, it is not unlikely that societies will strive to protect human development and coastal infrastructure, even if this results in the destruction or degradation of coral reefs. The result of these human actions will be to magnify the impacts that sea-level rise will have on corals and coral reefs in the affected coastal areas.

In summary, sea-level rise may provide candidate coral species with access to some new habitats by raising water levels above existing reef flats and by shoreward migration of coastlines. However, hardening of shorelines is likely to delay the progression of coastlines, and coastal inundation will likely release new sediments and pollutants into coastal reef waters, making some of these new habitats inhospitable to many coral species, as reported in fossil records (Blanchon et al., 2009). Other factors, including a lack of suitable new habitat or limited success in sexual recruitment, could also impair the ability of corals to keep up with sea-level rise. The influence of rising sea level on the 82 candidate coral species is likely to have mixed responses for the respective species depending on their depth preferences, sedimentation tolerances, growth rates, and the nearshore topography. Reductions in growth rate attributed to local stressors, bleaching, infectious disease, ocean acidification may prevent the species from keeping up with sea-level rise. Therefore, this threat is ranked as low to medium for all regions throughout these species’ ranges (Fig. 3.2.17).

3.2.5 Changing ocean circulation

In addition to their fundamental influences on heat storage and transport for the global climate system, ocean currents directly and significantly influence coral reef ecosystems through many important processes, including larval transport and recruitment dynamics (connectivity), nutrient enrichment (biomass productivity), heating and cooling (bleaching), and control of the basic biogeochemical processes, such as respiration, photosynthesis, and calcification (Fig. 3.2.18). 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.

The dominant, basin-scale wind-driven surface gyres are clockwise in the northern hemisphere and counterclockwise in the southern hemisphere in response to the Coriolis effect of the earth’s rotation. Many coral reefs are located in areas dominated by easterly trade winds. Being primarily wind-driven, the surface currents will respond to climate change-induced alterations in surface wind patterns across the tropics. As a result, these surface ocean currents are highly variable over a broad range of spatial and temporal scales, most notably seasonal and interannual time scales associated with the El Niño-Southern Oscillation (ENSO). ENSO events can influence larval availability and productivity of corals and other coral reef organisms. In reef regions that warm during El Niño (such as French Polynesia; Lo-Yat et al., 2011), El Niño leads to less productivity and a lower larval supply. The mean tropical atmospheric circulation is a large-scale zonal (east–west) overturning of air across the equatorial oceans—driven by convection to the west and subsidence to the east—known as the Walker circulation (Ries et al., 2006). Vecchi et al. (2006) examined changes in tropical Pacific circulation since the mid-19th century, using both observations and a suite of global climate model experiments and found a weakening of this Walker circulation. The size of this weakening trend is consistent with theoretical predictions and is accurately reproduced by climate model simulations that indicate it is largely a result of anthropogenic climate forcing (Vecchi et al., 2006). According to their climate model, the weakened surface winds have altered the thermal structure and circulation of the tropical Pacific Ocean. Ocean-color remote sensing has shown an expansion of zones of low productivity (oligotrophic waters) in most extra-tropical ocean areas, and this has been attributed to these circulation changes (Polovina et al., 2008). However, in another comparison of climate observations to models, Wentz et al. (2007) found that global and tropical ocean winds have been increasing over the last 20 years (though slower in the tropics), in contrast to models that indicate winds will weaken. Along with these changes in winds, models and observations both show an increase in atmospheric water vapor and precipitation (Wentz et al., 2007). Although these findings suggest that tropical wind-driven ocean currents will continue changing, the details about future directions and speeds of these surface currents remain insufficiently understood to adequately predict the potential influences to coral reefs generally or to the 82 candidate coral species in particular.

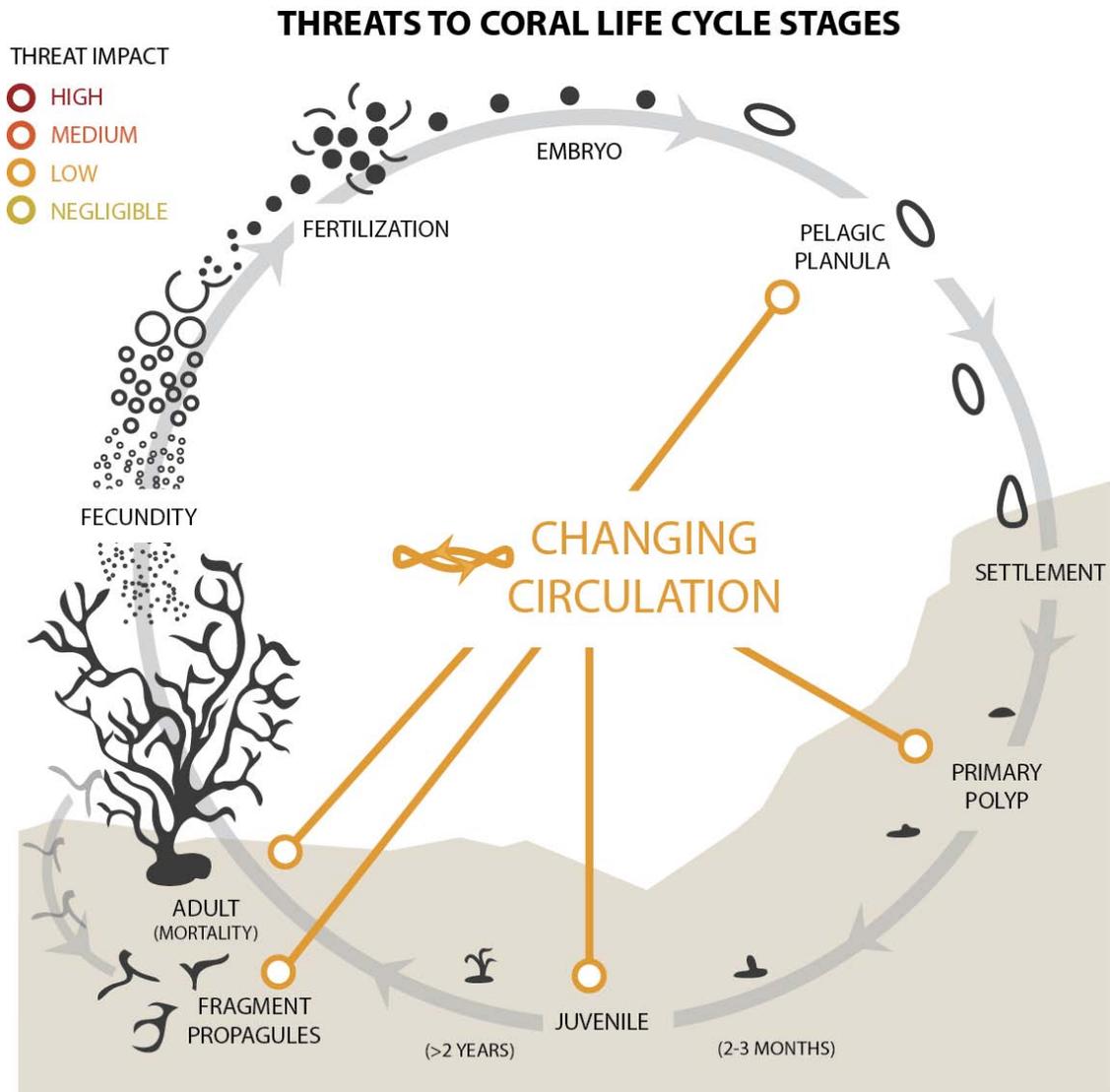


Figure 3.2.19. The impacts of changes in ocean circulation to various coral life history stages, including adult mortality and fragmentation, pelagic planula, polyp development, and juvenile growth. The overall contribution of changes in ocean circulation to the extinction risks of the 82 candidate coral species was determined to be **low** by the BRT. Diagram prepared by Amanda Toperoff, NOAA PIFSC.

As for the density-driven thermohaline circulation of the ocean interior, many general circulation models of the coupled ocean-atmosphere system predict that anthropogenic warming will lead to a potential weakening of Atlantic Thermohaline Circulation (Latif et al., 2000) through surface warming and freshening in high latitudes. Some models even suggest that sufficiently strong greenhouse gas forcing may result in a complete breakdown of the Thermohaline Circulation (Rahmstorf, 2002). In contrast, other climate models indicate that warming may lead to large-scale tropical air-sea interactions similar to those seen during present-day El Niño events, leading to anomalously high salinities in the tropical Atlantic that would be advected into the North Atlantic sinking region, counteracting local warming and freshening (Latif et al., 2000). The conflicting patterns of circulation under future warming makes it difficult to assess the likelihood of various future circulation scenarios, mainly owing to poorly constrained model parameterizations and uncertainties in the response of ocean currents to greenhouse warming (McMullen and Jabbour, 2009). Analyses of previous abrupt climate changes help resolve some of these problems (Rahmstorf, 2002). Data and models both suggest that abrupt climate change during the last glaciation originated through changes in the Atlantic Thermohaline Circulation in response to small changes in the hydrological cycle (McMullen and Jabbour, 2009). Atmospheric and oceanic responses to these changes were then transmitted globally through a number of complex feedbacks. The paleoclimatic

data and the model results also indicate that the Thermohaline Circulation is only stable under the current mean climate state (McMullen and Jabbour, 2009), which itself is undergoing dynamic global changes.

The BRT recognizes that rising atmospheric greenhouse gas concentrations and climate change may result in abrupt changes in basin-scale circulation patterns. Such changes could have significant and far-reaching global consequences. For example, connectivity between reefs is essential in terms of providing larvae to foster recovery from disturbance as well as long-term gene flow. However, while it appears likely that changes in ocean circulation patterns will occur, too much uncertainty in the modeling of ocean circulation in a changing climate remains to adequately incorporate the range of these potential changes into the risk assessments of the 82 candidate coral species.

3.2.6 Changing storm tracks and intensities

The IPCC consensus did not determine whether anthropogenic climate effects will change the average number of tropical cyclones, but they did anticipate a likely increase in tropical cyclone intensity (IPCC, 2007b): “Based on a range of models, it is *likely* that future tropical cyclones (typhoons and hurricanes) will become more intense, with larger peak wind speeds and more heavy precipitation associated with ongoing increases of tropical sea surface temperatures. There is less confidence in projections of a global decrease in numbers of tropical cyclones. The apparent increase in the proportion of very intense storms since 1970 in some regions is much larger than simulated by current models for that period.” Updated research continues to support this IPCC assessment (Knutson et al., 2008).

Under natural conditions, hurricane damage is one of many forms of disturbance that corals have experienced for millennia. However, other anthropogenic stresses to coral reef ecosystems (bleaching, sedimentation, eutrophication, ocean acidification, etc.) have reduced the ability of some coral reefs to return to their mean pre-disturbance state or condition by slowing coral recruitment, growth, and reducing fitness (Nyström et al., 2000). Already, bleaching and tropical storm disturbances have caused successive and substantial losses of elkhorn and staghorn coral cover in the Florida Keys (Miller et al., 2002; Williams et al., 2008a). Tropical storms can bring benefits to reefs if the storms pass far enough away to not inflict damage, but close enough to cool waters through enhanced wave-induced vertical mixing and reduce bleaching risk (Manzello et al., 2007; Szmant and Miller, 2005). Historically, tropical storms likely fostered propagation of elkhorn and staghorn coral thickets through fragmentation, but recent observations from periods of frequent hurricanes in the Florida Keys document a lack of successful recruitment of fragments and a severe population decline (Williams et al., 2008a). A recent modeling study out to 2099 predicted that Caribbean coral reefs are likely to maintain their community structure and function under any expected level of hurricane activity, at least under (perhaps unlikely) conditions with high herbivory and minimal thermal bleaching (Edwards et al., 2010).

Buddemeier et al. (2004) argued that there is little evidence for projected changes in storm frequency and there is no agreement on an increase of storm intensity with projected global climate change. However, there is general agreement that hurricane frequency increased in the mid-1990s, after a 30-year lull in activity, back to levels experienced earlier in the 20th century. Goldenberg et al. (2001), in evaluating various studies comparing hurricane frequency changes and global climate change, stated that the data are as of yet inconclusive. Some models indicate that tropical cyclones in the Pacific might increase in intensity by 5% to 12% (Knutson et al., 2001), although that study did not address the applicability of their results to other ocean basins. Others have highlighted the uncertainty in concluding that regional hurricane frequencies are not yet predictable (Henderson-Sellers et al., 1998). That study also concluded that intensities will likely remain the same or increase at a modest 10% to 20%, stating that these predicted changes are small compared with natural variations. Still others modeling the effects of greenhouse gas-induced warming have found that the frequency of storms would be significantly reduced (Bengtsson et al., 1996). Although there is no clear evidence for or against future changes in storm frequency associated with global climate change (2004), there is greatest agreement that climate change will increase tropical storm intensity (Knutson et al., 2008). Any change in frequency would affect the time available for coral recovery from storm damage, although other anthropogenic changes (acidification, sediment stress, etc.) could also change the length of time corals require to recover from storm disturbances. All things considered, the BRT determined changes in tropical storm frequency and intensity to represent a low but uncertain level of threat to the extinction risks for the 82 candidate coral species.

3.2.7 African and Asian dust

Scientists have long known that dust clouds travel long distances. Soils found on many Caribbean islands may have been substantially enriched with iron from African dust (Garrison et al., 2003), and studies show that essential nutrients in Hawaiian rainforests are transported via dust from Asia (Kurtz et al., 2001). Hundreds of millions of tons of dust transported annually from Africa and Asia to the Americas may be adversely affecting coral reefs and other downwind

ecosystems (Garrison et al., 2003). Viable microorganisms, macro- and micronutrients, trace metals, and an array of organic contaminants carried in the dusty air masses and deposited in the oceans and on land could affect coral reefs worldwide. Shinn et al. (2000) proposed that atmospheric dust transported largely from Africa has severely affected Caribbean coral-reef organisms by acting as a vector for pathogens such as *Aspergillus sydowii*, a fungus known to affect two sea fans (*Gorgonia ventalina* and *Gorgonia flabellum*) (Geiser et al., 1998). Recent research, however, found that of seven species of *Aspergillus* present in dust samples collected from Mali and St. Croix in the U.S. Virgin Islands, *Aspergillus sydowii* was not present (Rypien et al., 2008). Several other studies that examined the fungal biota of African dust also did not detect *Aspergillus sydowii*, although several other species of *Aspergillus* were present (Griffin et al., 2003; Kellogg et al., 2004; Shinn et al., 2003; Weir-Brush et al., 2004). These data taken in conjunction with recent molecular evidence, suggest that African dust as a source of the marine pathogen *Aspergillus sydowii* should be considered unlikely (Rypien et al., 2008). To date, the identified (*Serratia marcescens*) or suspected (*Vibrio charcharia*) pathogens of elkhorn and staghorn corals have not been identified among the microbes in dust (Griffin et al., 2002). Therefore, the BRT ranked the threat posed by African and Asian dust as negligible for all areas throughout the ranges of the 82 candidate coral species, and left unabated, this threat is not expected to significantly increase the extinction risk for any of these species. There is also no well-established connection between anthropogenic climate change and future levels of African or Asian dust.

3.2.8 Changes in insolation

Since the late 1950s, a global network of solar radiation measurements at the Earth's surface have revealed that the energy provided by the sun at the Earth's surface has undergone considerable variations over the past decades, with associated impacts on climate (Ohmura, 2009; Wild, 2009). Wild (2009) reported that solar radiation at the Earth's surface decreased by 2% per decade between the 1950s and 1990 and increased from 1985 to the present (Wild, 2009); he coined the two phrases "global dimming" and "global brightening" to describe these trends.

No evidence shows that solar radiation reaching the upper atmosphere has changed. Instead, changes in surface irradiance appear to have been the result of light absorption in the atmosphere. However, it is unclear how much global dimming/brightening can be attributed to clouds and water vapor, aerosols, and interactions between clouds and aerosols, as aerosols can influence the "brightness" and lifetime of the clouds by providing cloud condensation nuclei. The investigation of these relationships is complicated by the fact that insufficient—if any—observational data are available on how clouds and aerosol loadings have been changing over the past decades. Another unresolved question is what happens over the oceans, as barely any high-quality insolation data are available from over water or even on islands. A further challenge is to incorporate the effects of global dimming/brightening more effectively in climate models, to better understand their effect on climate change. Modeling and attribution studies indicate that global dimming attributed to increased aerosols masked the actual temperature rise—and therefore climate change—until well into the 1980s (Streets et al., 2006). Moreover, the studies also show that the models used in the IPCC Fourth Assessment Report (IPCC, 2007b) do not fully capture the measured effects of global dimming/brightening (Wild and Liepert, 2010). This is probably because of a limited understanding of the processes causing global dimming/brightening and the considerable uncertainties about historical levels of anthropogenic pollutants used as model input (Wild and Liepert, 2010). Also problematic was the limited quality of insolation data prior to the 1990s (Wild, 2009).

If aerosols and their interactions with clouds were the primary cause of dimming, a large part of current brightening is related to legislation and policies that have reduced air pollution. Therefore, brightening is likely a restoration of insolation levels that would have existed without industrial pollution. Global dimming/brightening have thus far resulted in changes in insolation at the ocean surface of about 2% per decade (Wild, 2009). As light is absorbed exponentially with depth in seawater, with attenuation dependent on the wavelength of light and water column characteristics such as turbidity, colored dissolved organic matter, and plankton, it is anticipated, although far from certain, that these relatively small changes surface insolation will likely have minimal effect on corals. That said, it is well understood that corals and coral reefs, and most marine life, are dependent on and are sensitive to incoming solar radiation to drive photosynthesis and heat flux into the ocean. Unfortunately, the current state of our knowledge about future changes in surface solar radiation and the ecological responses of such changes remain too uncertain for the BRT to effectively incorporate into analyses about the Critical Risk Thresholds for the 82 candidate coral species.

3.2.9 Summary of global changes and their impacts

Rising atmospheric CO₂, and its concomitant impacts on the oceanic environment, has already contributed to the deterioration of coral reefs and coral species populations globally (Hoegh-Guldberg et al., 2007; Wilkinson, 2008). By the early 1980s, atmospheric CO₂ levels had risen from preindustrial levels of about 280 ppm to in excess of 340 ppm. Thermal stress began causing mass coral bleaching events in the 1980s and became a global problem in the 1990s. By the 1990s, the return frequency of mass bleaching in parts of the Caribbean was exceeding the ability of many reefs and coral species to recover from bleaching and disease effects (Eakin et al., 2010), and the combination of stressors were decreasing coral reef architectural structure (Alvarez-Filip et al., 2009). Coral disease outbreaks first began in some locations in the Caribbean Sea in the 1970s (Bak and Criens, 1982; Gladfelter, 1982) and were followed by major outbreaks across the entire Caribbean Sea (Aronson and Precht, 2001). Presently, atmospheric CO₂ levels exceed 390 ppm and this high concentration likely has contributed to the decline of many coral reefs through processes described herein. Human activities are releasing CO₂ into the atmosphere rapidly and this rate is expected to increase, exceeding worst case scenarios used in modeling future climate change (IPCC, 2007b; WDCGG, 2010).

Some experts have suggested that atmospheric CO₂ levels must be reduced to those found in the 1970s (below 340 ppm and perhaps as low as 320 ppm) to maintain healthy coral growth over the long term (Veron et al., 2009). Because natural rates of CO₂ sequestration are much slower than rates of anthropogenic CO₂ increase, there are significant time lags between changes in atmospheric CO₂ levels and stabilization of temperature and ocean pH. Due to these delays, many of the ecological effects of anthropogenic CO₂ increases will not be evident for many years. This fact may cause governments to postpone remedial actions and further extend the time during which conditions are unfavorable to corals and coral reefs (Medina-Elizalde et al., 2002).

During this century, rising atmospheric CO₂ will continue to induce thermal stress and ocean acidification, which likely represent severe threats to the long-term growth and survival of many coral species and coral reefs more generally. This global stressor will likely influence, to varying degrees, many or most of the 82 candidate coral species throughout all or most of their ranges. However, the severity of ocean acidification has only become apparent within the last decade. There is still much that we need to know to understand how this threat will affect the particular species under consideration and various other important components of the reef ecosystem. Based on our current knowledge and projections for the future, acidification is ranked as medium-high for all areas throughout the ranges of the candidate coral species. The severity of this threat to the growth and recruitment of corals will make it more difficult for them to recover as their populations are affected from other threats, such as bleaching. Thermal stress and associated bleaching and disease are already causing widespread coral mortality events and may have caused the first recent coral extinction (Glynn et al., 2001). Effects of bleaching vary with region, species, and prior exposure, and corals may have some modest capacity to adapt or acclimate to changing thermal conditions. However, field observations and models both predict that the frequency and severity of bleaching is increasing, inducing greater mortality and allowing less time for recovery. Between the direct (e.g., bleaching) and indirect (e.g., infectious disease) effects of rising temperatures, climate change has already had negative consequences on many coral species, and this is expected to continue and accelerate as atmospheric CO₂ continues to rise. The highly certain threat of continued warming to the 82 candidate coral species is, therefore, considered high for most regions where these corals are known to occur. The combined direct and indirect effects of rising temperature, including increased incidence of disease and ocean acidification, both resulting primarily from anthropogenic increases in atmospheric CO₂, are likely to represent the greatest risks of extinction to all or most of the candidate coral species over the next century.

3.3 Local Threats to Coral Species

3.3.1 Land-based sources of pollution

A decade ago, it was estimated that 58% of the world's coral reefs were potentially threatened by human activities such as coastal development, resource exploitation, and land-based and marine pollution (Bryant et al., 1998). A more recent assessment indicated that the situation has continued to deteriorate, as coastal human populations and their collective consumption of natural resources have continued to increase unabated (Burke et al., 2011). Human activities in coastal watersheds introduce sediment, nutrients, chemical contaminants, and other pollutants into the ocean by various mechanisms, including river discharge, surface runoff, groundwater seeps, and atmospheric deposition. Humans introduce sewage into coastal waters through direct discharge, treatment plants, and septic leakage, each bringing nutrients and microbial contamination. Agricultural runoff brings additional nutrients from fertilizers, as well as harmful

chemicals such as pesticides. Elevated sediment levels are generated by poor land-use practices. Industry is a major source of chemical contaminants, especially heavy metals and hydrocarbons.

Several seminal review papers have described the effects of coastal pollution on coral reefs and provide a more detailed treatment of the topic than space allows here. These works include the effects of sewage (Pastorok and Bilyard, 1985), sedimentation (Rogers, 1990), nutrient enrichment (Dubinsky and Stambler, 1996; Szmant, 2002), terrestrial runoff (Fabricius, 2005), and contaminants (Peters et al., 1997). Many of these water quality parameters and their consequent biological effects co-occur in the field, making it difficult to definitively establish causative mechanisms (Fabricius, 2005). The situation is further confounded by the fact that some pollutants have both direct and indirect effects, while others may be beneficial in small amounts but are detrimental at elevated levels.

The BRT acknowledges that these factors interact in complex ways and considered the holistic nature of threats in the species evaluations. All land-based sources of pollution were considered to act at primarily local and sometimes regional levels, with direct linkages to human population and resource consumption, as well as land use, within the local and regional areas. These linkages are logically presumed (e.g., in predictive or correlative modeling studies such as Bryant et al., 1998; Burke et al., 2011; Mora, 2008), but also supported by correlational and retrospective studies of both threat dosage of and coral response to land-based sources of pollution (Carilli et al., 2009a; Dinsdale et al., 2008; McCulloch et al., 2003) and landscape development (Oliver et al., 2011). Overall, pollution poses substantial extinction risks primarily to species with limited geographic and habitat distributions. Local stresses can be sufficiently severe to cause local extirpation or interact with global stresses to alter extinction risks. For clarity of presentation, four classes of pollutants/stressors are examined below: sedimentation, nutrients, toxins, and salinity.

3.3.1.1 *Sedimentation*

There are two basic types of sediments that influence coral reefs: those that are terrestrially derived and those that are generated in situ through erosion and the skeletal material of calcifying organisms (corals, mollusks, *Halimeda*, foraminifera, etc.). Delivery of terrestrial sediment is likely to be the most pervasive sediment stress that corals experience, though dredging, beach re-nourishment, and winds and seas that remobilize in situ sediments can also result in important stresses to corals in some areas. Terrestrial sediments are also likely to have greater impacts than marine sediments because of their physical and chemical characteristics. Terrestrial sediments tend to be both finer (more easily resuspended) and darker (more light-absorbing); consequently terrestrial sediments reduce light more effectively than marine sediments when suspended in the water column (Te, 1997). The high iron content of some terrestrial sediments may serve as fertilizers to certain components of some coral reef systems. Terrestrial sediments are also often associated with harmful organic compounds, heavy metals, nutrients or harmful bacteria (Bastidas et al., 1999; Hodgson, 1990; Jokiel et al., 2004). These associated constituents, combined with grain size and organic content, are primary factors in determining sedimentation stress in corals (Weber et al., 2006).

Exposure, including both the amount of sediment and the duration of the sediment stress, are also primary factors in determining the effects of sediments on corals (Philipp and Fabricius, 2003). Sediments are delivered during episodic events such as storms that create turbid plumes that may persist for several days (Storlazzi et al., 2009; Wolanski et al., 2003). In some reef systems, prevailing ocean swells and tidal currents flush out and remove sediment deposits from the reefs over periods of weeks or months (Larcombe et al., 1995; Storlazzi et al., 2009; Wolanski et al., 2005), while major storms and associated swell can move large amounts of sediment during pulse events in a matter of hours or days (Dollar and Grigg, 2004; Hubbard, 1986; 1992). In areas dominated by trade winds rather than longer period ocean swell, fine sediments may be repeatedly resuspended but not transported out of the system, repeatedly disturbing the same reef for years or decades (Ogston et al., 2004; Presto et al., 2006; Storlazzi et al., 2004). However, increases in sediment supply would not result in greater turbidity or sediment deposition on reefs where these processes are controlled more by local hydrodynamics than sediment inputs (Larcombe et al., 2001; Larcombe and Woolfe, 1999).

The most common direct effect of sediment (Fig. 3.3.1) is deposition on the coral surface, as sediment settles out from the water column and is greatly affected by varying characteristics of both the coral colonies and the sediment. Corals can passively reject settling sediments, based on colony morphology or actively displace sediment by ciliary action or mucus production (Bak and Elgershuizen, 1976; Dallmeyer et al., 1982; Lasker, 1980; Stafford-Smith, 1993; Stafford-Smith and Ormond, 1992), both requiring energetic expenditures by the corals. Corals with large calices tend to be better at actively rejecting sediment (Stafford-Smith and Ormond, 1992). Some coral species can tolerate complete burial for several days (Rice and Hunter, 1992). If the corals are unsuccessful in removing the sediments, they can become smothered and die (Golbuu et al., 2003; Riegl and Branch, 1995; Rogers, 1983). The ability of solitary

Fungia sp. to survive sediment burial is size-specific (Gilmour, 2002), and massive Caribbean corals show high rates of partial mortality in sediment-affected areas (Nugues and Roberts, 2003), although this may simply reflect a tendency for small colonies to show total rather than partial mortality (Dudgeon et al., 2010).

In addition to direct mortality, sediment can induce sublethal effects, such as those revealed histologically as cellular/structural disruptions (Vargas-Ángel et al., 2007), reduced tissue thickness (Flynn et al., 2006), polyp swelling, zooxanthellae loss, and excess mucus production (Marszalek, 1981). Active removal of sediment deposited on the coral surface comes at an energetic cost—respiration increases, photosynthetic efficiency decreases, and photosynthesis/respiration ratio decreases (Anthony and Connolly, 2004; Dallmeyer et al., 1982; Philipp and Fabricius, 2003; Riegl and Branch, 1995; Te, 2001; Telesnicki and Goldberg, 1995; Weber et al., 2006). Suspended sediment can reduce the amount of light in the water column, making less energy available to the coral for photosynthesis and growth (Anthony and Hoegh-Guldberg, 2003; Bak, 1978; Rogers, 1979) or restricting the corals to shallower waters than might otherwise be the case (Yentsch et al., 2002). Sediment impedes fertilization of spawned gametes (Gilmour, 1999; Humphrey et al., 2008) and reduces both larval settlement and survival of recruits and juveniles (Birrell et al., 2005; Fabricius et al., 2003; Fukami et al., 2004; Hunte and Wittenberg, 1992). Thus, corals may be forced to rely more heavily on asexual recruitment as larger (fragment) propagules should be less vulnerable to sediment smothering than larvae (Highsmith, 1982).

The net effects of sediment impacts at coral community levels are reductions in coral cover and shifts toward more sediment-tolerant species assemblages (Acevedo et al., 1989; Brown et al., 1990; Fig. 3.3.1; Cortes and Risk, 1985; Dodge and Vaisnys, 1977; Loya, 1976). Some of these communities can have relatively high coral cover or diversity and can withstand very high rates of short-term sediment accumulation (Larcombe et al., 2001). Species that are more sediment-tolerant tend to be those that are more efficient sediment rejecters (Stafford-Smith, 1993) or those that can shift to a greater reliance on heterotrophy, such as sediment ingestion (Anthony, 1999; Anthony and Fabricius, 2000; Anthony and Larcombe, 2000; Mills et al., 2004), and are often species that can tolerate a wide range of environmental conditions. These community-level changes are generated by direct and indirect effects, from sediment settling to the seafloor or turbid conditions in the water column.

It is difficult to quantitatively predict the extinction risks posed by sediment stresses. Human activity has resulted in quantified increases in sediment inputs to the Great Barrier Reef over the past century and a half (McCulloch et al., 2003), as has likely occurred elsewhere. Continued increases in human populations in coastal areas, combined with poor land-use practices, will likely increase sediment delivery to other coastal and high island coral reef areas. Nearshore sediment levels will likely increase, possibly greatly, with projected sea level rise (see Section 3.2.4.2). Greater inundation of reef flats can erode soils at the shoreline and resuspend lagoon deposits (Adey et al., 1977; Lighty et al., 1978), thereby producing greater terrestrially-derived sediment transport (Hopley and Kinsey, 1988). Combined, this potentially leads to leeward reefs being “shot in the back by their own lagoons” (Neumann and Macintyre, 1985) as they are flooded with turbid lagoon waters or buried by off-bank sediment transport (see also Section 3.2.4.2). For example, fossil records indicate a 2–3 m sea-level rise may have enhanced wave energy and sediment flux, eroding and burying corals in lagoonal reefs in Mexico at the time of the last interglacial period, although it can also lead to a change in coral community structure with more sediment-tolerant species (Blanchon et al., 2009). Alternatively, turbid areas could serve to enhance coral survival. Over geologic time, turbid inshore habitats have been continually available, providing continuity and refugia for scleractinian corals during non-reef periods (Potts and Jacobs, 2000). Some evidence indicate that bleaching-induced mortality may be lower in turbid areas (Brown, 2007; Goreau et al., 2000; Jokiel and Brown, 2004), as corals in these areas may host more stress-tolerant zooxanthellae (LaJeunesse et al., 2010) or more stress-tolerant species may be more predominant in sediment-prone reef areas. However, sediment stress and turbidity can also induce bleaching (Philipp and Fabricius, 2003; Rogers, 1979). Increased pigment levels in corals adapted to turbidity can also predispose them to greater tissue temperatures when environmental conditions are conducive to bleaching (Fabricius, 2006). Considering all of the above information, the BRT assessed the overall extinction risks of the 82 candidate coral species based on sedimentation stress to be low to medium.

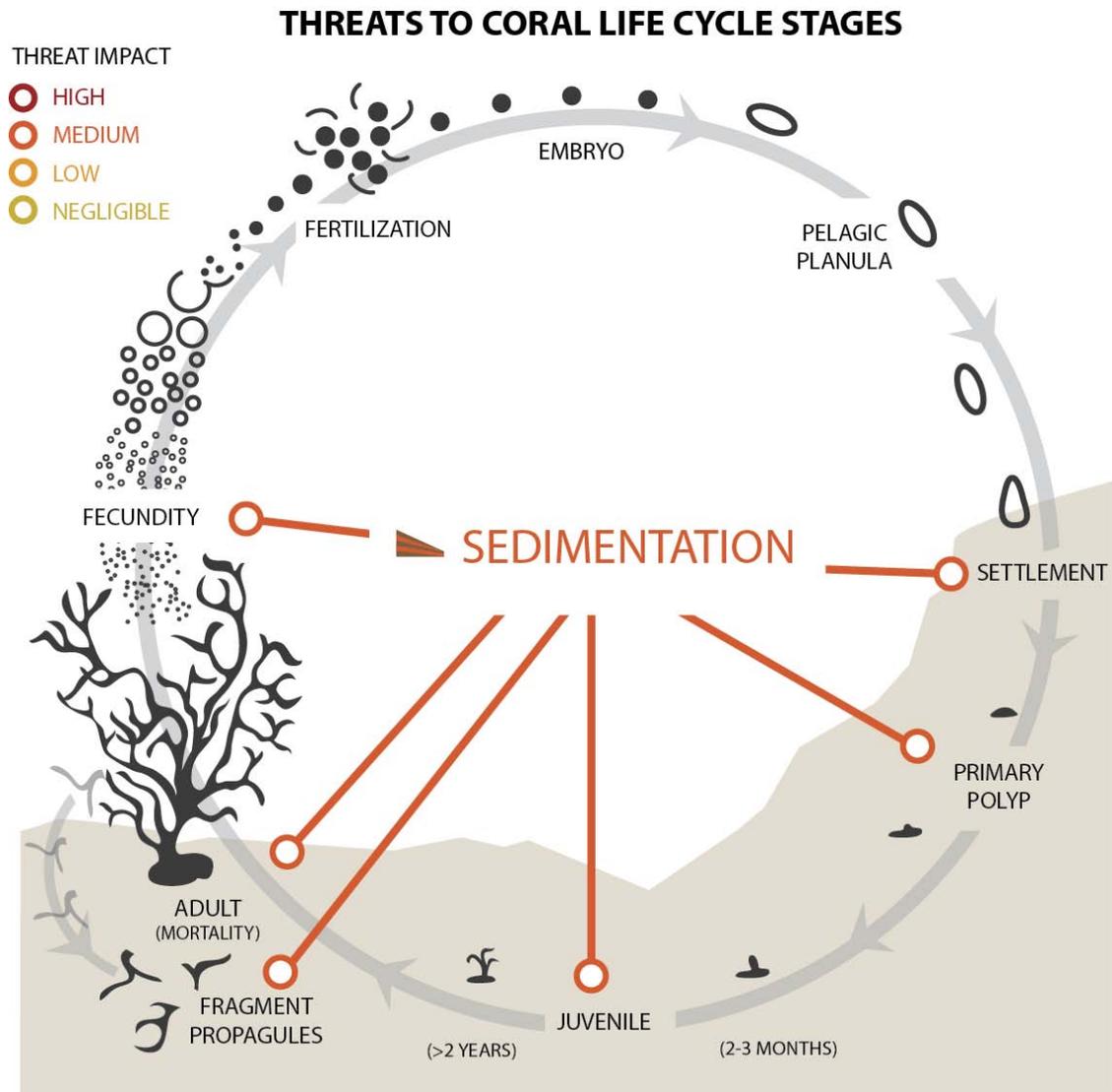


Figure 3.3.1. The impacts of sedimentation stress to various coral life history stages, including adult fecundity and fragmentation, settlement, and juvenile growth. The overall contribution of sedimentation to extinction risk for the 82 candidate coral species was determined to be low-medium by the BRT. Diagram prepared by Amanda Toperoff, NOAA-PIFSC.

3.3.1.2 *Nutrients*

Nutrients are chemicals that organisms need to live and grow or substances used in an organism’s metabolism which must be acquired from the surrounding environment. This makes the availability of nutrients highly influential in the function and status of organisms and ecosystems, as too few nutrients is limiting but too many nutrients can result in detrimental ecological imbalances. The traditional view of coral reefs is that they thrive in nutrient-poor oceanic waters because of the tight recycling between the host coral and its symbiotic zooxanthellae (Muscatine and Porter, 1977). While oceanic surface waters might indeed be oligotrophic, there are multiple sources of natural nutrients to coral reefs, such as in situ nitrogen fixation (Wiebe et al., 1975) and delivery of nutrient-enriched deep water by topographic and internal wave-induced upwelling (Leichter et al., 1996; Wolanski and Delesalle, 1995) and by reef endo-upwelling (Rougerie and Wauthy, 1993). These natural sources may account for more material (nitrogen and phosphorus) than estimates of anthropogenic sources (wastewater plus stormwater) in highly developed areas such as the Florida Keys (Leichter et al., 2003). As was briefly discussed in Section 3.2.2.3, predicted ocean warming is expected to cause increased stratification of the upper ocean which will decrease vertical mixing of both heat (warmer water down and cooler water up) and nutrients, leaving surface waters warmer and less nutrient-enriched (Behrenfeld et al., 2006).

Natural mechanisms for delivering nutrients to coral reef areas are sometimes enriched by anthropogenic activities. Although groundwater inputs are highly variable, they can be significantly nitrogen-enriched (D'Elia et al., 1981; Paytan et al., 2006). Groundwater was estimated to supply 5%–35% of the nitrogen inputs to reefs in Ishigaki, while atmospheric deposition was generally < 1% (LaJeunesse et al., 2004b). Atmospheric nitrogen deposition was estimated to supply ~ 20% of the nitrogen necessary for growth of reef macroalgae in the Bahamas where surrounding waters are oligotrophic and anthropogenic input is low, nitrogen deposition rates in more populated Florida, however, were about four times higher (Barile and Lapointe, 2005). The main vectors of anthropogenic nutrients are point-source discharges (such as rivers or sewage outfalls) and surface runoff from modified watersheds. The majority of these nutrient sources may also bring other stressors (e.g., sediments, turbidity, contaminants), which are discussed in other sections of this document.

When nutrient levels rise in coral reef systems, plant growth can be expected to increase and this can result in ecological imbalances and changes in community structure. This may be particularly the case when herbivory has been reduced, as by disease or fishing on herbivorous fishes. Elevated nutrients affect corals through two main mechanisms—direct impacts on coral physiology, and indirect effects through nutrient-stimulation of other community components, such as macroalgal turfs and seaweeds, and filter feeders, that compete with corals for space on the reef.

Direct effects of nutrients on corals are mediated by the symbiotic relationships between the corals and their zooxanthellae. Excessive nutrient enrichment can disrupt the symbiosis (Dubinsky and Stambler, 1996), thereby affecting metabolic processes, coral growth, and reproductive success. Fast-growing branching corals may be more susceptible to internal nutrient effects than slower-growing massive corals (Maté, 1997; Schlöder and D'Croz, 2004). Increased nutrient levels generally lead to an increase in zooxanthellae density and/or chlorophyll content (Hoegh-Guldberg and Smith, 1989b; Muscatine et al., 1989a), which stimulates photosynthesis (Marubini and Davies, 1996). However, this supplemental energy is retained more by the symbionts for their own propagation, while the energy transferred to the coral host declines (Falkowski et al., 1993). These uneven distributions of energy may even increase the susceptibility of corals to high temperatures, thus increasing bleaching (Wooldridge, 2009a; Wooldridge and Done, 2009). Laboratory manipulations with elevated nitrogen and phosphorus have shown decreased calcification, sometimes with greater reduction in combination than either alone (Ferrier-Pages et al., 2000; Marubini and Davies, 1996). Nutrients may enhance linear extension but reduce skeletal density, making corals more prone to breakage or erosion (Koop et al., 2001; Tomascik, 1990; Tomascik and Sander, 1985).

Elevated nutrient levels are generally detrimental to coral reproduction, although the stage at which effects occur may be both species-specific and nutrient-specific. In general, elevated nutrient levels have been found to inhibit gamete development, shift towards more male gametes, reduce fertilization success, reduce larval settlement, and thus increase reliance on asexual reproduction (Harrison and Ward, 2001; Loya et al., 2004; Rinkevich and Loya, 1979b; Tomascik and Sander, 1987b; Ward and Harrison, 2000). When elevated nutrients do not reduce fertilization on their own, they may do so in concert with other factors such as salinity (Humphrey et al., 2008) or affect a different portion of the reproductive cycle than was tested (Loya and Kramarsky-Winter, 2003). Coral reproductive mode may also modulate nutrient response; for example, the brooding coral *Pocillopora damicornis* ceased planula production after several months of ammonium enrichment, but the broadcast spawner *Montipora capitata* (whose eggs contain zooxanthellae) showed no reduction in fecundity (Cox and Ward, 2002) under the same conditions. Reefs in eutrophic waters have been shown to have lower densities of juveniles (Tomascik, 1991), possibly as a result of lowered post-settlement survivorship.

Corals may have some capacity to physiologically adapt to long-term nutrient conditions in aquaria (Atkinson et al., 1995; Yuen et al., 2008), but in the field, the more important effects are likely to be indirect, namely stimulation of non-coral components of the reef system and alteration of the competitive balance on the reef. Nutrient enrichment can stimulate the production of particulate matter such as plankton, leading to an increase in sponges, zoanths, and other filter feeders (Bell, 1991; Costa et al., 2008). As the most destructive bioeroding organisms are filter-feeders, increased nutrients may increase productivity in bioeroders and shift reefs from net accretion to net erosion (Hallock and Schlager, 1986).

More commonly, increased growth rates of free-living reef algae (e.g., turfs and seaweeds) might be expected to yield higher abundances and overgrowth of reef substrates. Indeed, the widespread increase in seaweed abundance on coral reefs in many populated areas has often been attributed to nutrient enrichment (Bell, 1991; Lapointe, 1997). However, experimental nutrient addition in some reef systems has not resulted in algal overgrowth (Grigg, 1995; Miller et al.,

1999; Thacker et al., 2001) because of the control of macroalgal standing stock by herbivores. A recent meta-analysis comparing nutrient and herbivory effects indicates 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). Nonetheless, the role of nutrient enrichment in reef community phase-shifts remains controversial (Hughes et al., 1999a; Lapointe, 1999; Szmant, 2002).

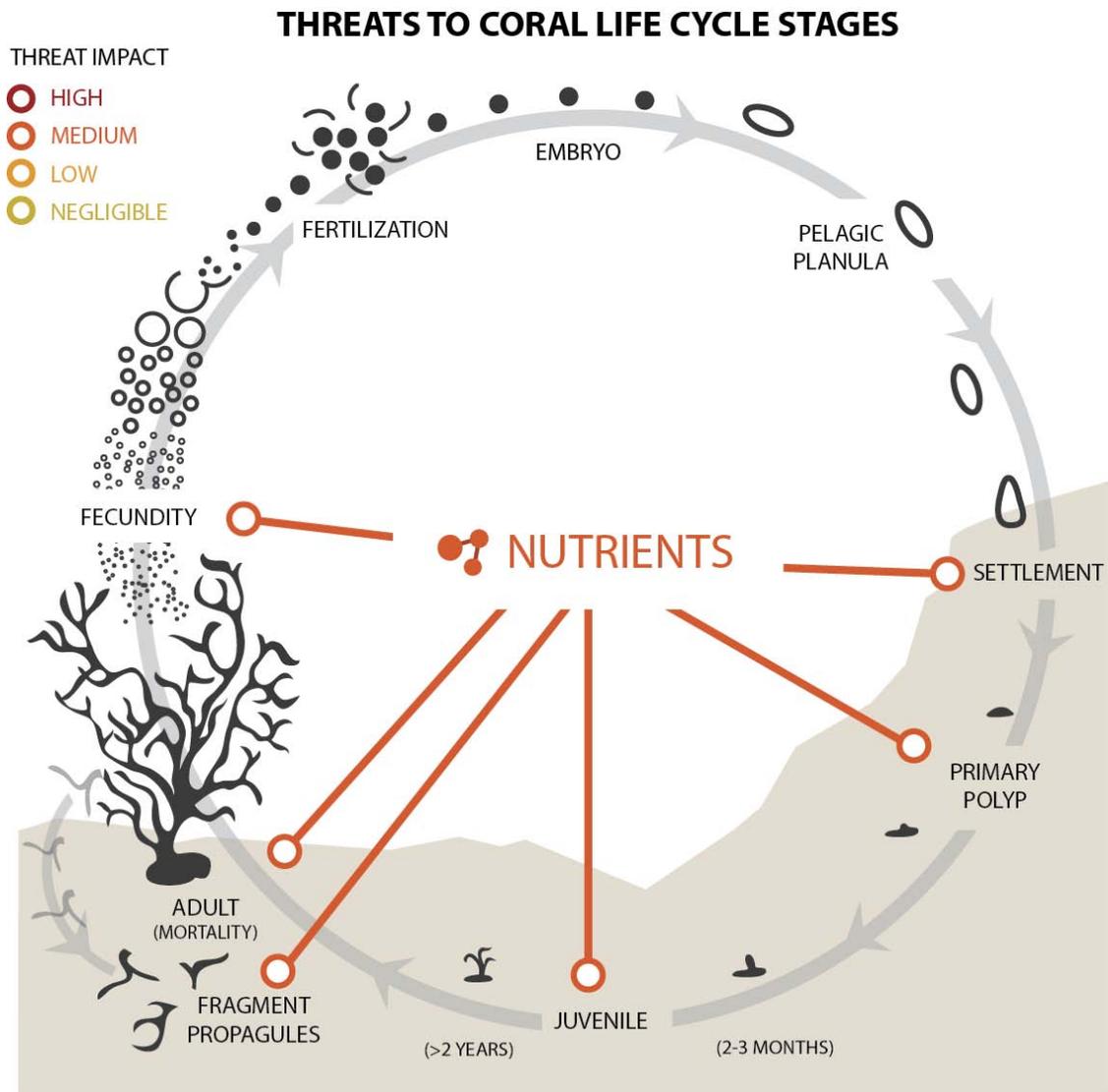


Figure 3.3.2. The impacts of nutrient stresses to various coral life history stages, including adult mortality, fecundity, and fragmentation, settlement, and juvenile growth. The overall contribution of nutrients (eutrophication) to extinction risk for the 82 candidate coral species was determined to be **low-medium** by the BRT. Diagram prepared by Amanda Toperoff, NOAA-PIFSC.

The mechanisms of direct competition between algae and corals are reasonably well-defined (Jompa and McCook, 2003; McCook et al., 2001), but less-apparent mechanisms involving allelopathy and microbial stimulation on both adult and larval corals are also beginning to be realized (Kuffner et al., 2006; Rasher and Hay, 2010; Smith et al., 2006). However, the effects on corals vary with the functional form of algae or often on the species within that functional form. For example, coral larvae settle at high rates in algal turfs and crustose coralline algae and at lower but variable rates when in contact with fleshy macroalgae (*Laurencia* and *Hypnea* differed substantially in the degree to which they inhibited coral settlement; Diaz-Pulido et al., 2010). Coral species likely also vary in their susceptibility to macroalgal inhibition, but this has rarely been a focus of experimental studies (Nugues et al., 2004a).

Ultimately, the net effects of nutrient enrichment and associated stresses on coral populations are a reduction in coral cover, shifts in coral community composition, and, under at least some conditions (e.g., reduced herbivory and/or restricted hydrodynamic circulation), increased algal biomass (Lapointe et al., 2010; Nairn, 1993; Tomascik and Sander, 1987a; Wielgus et al., 2004). Perhaps the best known example of deleterious effects of increased nutrient levels is sewage discharge directly into Kāneʻohe Bay, Hawaiʻi, where eutrophication in an enclosed basin with relatively long residence time led to outbreaks of the bubble alga *Dictyosphaeria cavernosa* and reduction in coral cover throughout much of the bay; the system recovered, but incompletely, after the sewage was diverted (Hunter and Evans, 1995; Maragos et al., 1985).

Establishing nutrient concentration thresholds to indicate eutrophic water quality may have little validity (McCook, 1999), but the evidence suggests that chronically elevated nutrient levels, particularly in the common modern conditions of reduced herbivory or in particular geographic locations with restricted water circulation, may alter reef function enough to cause changes in coral communities (Fabricius, 2005). However, extrapolating from community changes to extinction risk of individual species is complicated by poorly understood interactive effects. For example, bleaching, reductions in herbivory, and increased sediment stress can exacerbate even low-level nutrient inputs (Szmant, 2002), while eutrophication can slow recovery of corals from both natural and anthropogenic disturbances (Wielgus et al., 2003). Distance from shore or from human populations is not always a useful predictor of nutrient impacts either. Nearshore patch reefs in the Florida Keys have elevated nutrients and turbidity, but had higher coral cover, higher growth rates, lower partial mortality, and population size structures with more larger colonies than offshore reefs that had undergone greater recent degradation as a result of bleaching and disease (Lirman and Fong, 2007). Coral skeletons from Australia's Great Barrier Reef and the Flower Garden Banks in the Gulf of Mexico show evidence of runoff events (Deslarzes and Lugo-Fernandez, 2007; Isdale et al., 1998), although nutrient effects, per se, were not quantified. Excess nutrients are patchily distributed, and their multiple layers of indirect effects are contingent on many local environmental factors, such as hydrodynamics. For the purposes of this review, the BRT considers excess nutrients to produce low-to-medium extinction risks for the 82 candidate coral species.

3.3.1.3 *Toxins and contaminants*

As is the case with the other pollutant stressors (with which they co-occur), toxins and bioactive contaminants may be delivered to coral reefs via either point or non-point sources. Several reviews have been conducted on contaminants, including heavy metals, synthetic organics, and petroleum products (Howard and Brown, 1984; Loya and Rinkevich, 1980; Pait et al., 2007; Peters et al., 1997). However, the analytical ability to detect contaminants sheds little insight on the ecological effects that contaminants might have on corals. A substantial body of literature documents bioaccumulation of contaminants, and over the previous decade scientists have developed sophisticated molecular techniques as biomarkers (Downs et al., 2005; Morgan et al., 2005). The presence or constituent changes in a biomarker under exposure to a toxicant stress may provide some mechanistic understanding of the organismal response, but only if these mechanisms are well established in basic physiology and traditional dose-response experiments. Instead, effects to corals to date have most often been inferred from environmental correlations.

Records of heavy metals in skeletal material are primarily useful for evaluating the effects of long-term chronic exposures, such as contaminated sediment and runoff. For example, skeletal heavy metals were correlated with reduced coral growth rates near areas of coastal development in Jordan (Al-Rousan et al., 2007), rum refineries in Barbados (Runnalls and Coleman, 2003), tin smelter effluent in Thailand (Howard and Brown, 1987), and effects of agriculture and development on marine reserves along the Mesoamerican Reef (Carilli et al., 2010; Carilli et al., 2009b). Metals can be transported at long distances by ocean circulation, affecting even "pristine" reefs (Guzmán and García, 2002). Heavy metals bioaccumulate in coral host tissues and are most heavily concentrated in the zooxanthellae (Reichelt-Brushett and McOrist, 2003). Tissue body burden may far exceed concentrations found in skeletal material (Bastidas and Garcia, 1997; McConchie and Harriott, 1992), and the contaminants in tissues are in a position to more directly affect coral physiology. However, it is difficult to generalize responses to metal contamination because effects can be species-specific or moderated by exposure history. For example, when exposed to copper *Acropora cervicornis* and *Montastraea faveolata* accumulated the metal in their tissues but *Pocillopora damicornis* did not, while only *Acropora cervicornis* and *Pocillopora damicornis* showed reduced photosynthesis and growth (Bielmyer et al., 2010).

Elevated levels of iron have resulted in expulsion of zooxanthellae from *Porites lutea*, but corals exposed to daily runoff enriched with iron had a reduced response, suggesting that corals may be capable of adapting somewhat to exposure (Harland and Brown, 1989). And although bleaching is a generalized stress response, heavy metals can directly induce coral mortality in the absence of bleaching (Mitchellmore et al., 2007).

Other demonstrated sublethal effects of heavy metals include induction of heat shock proteins (Venn et al., 2009) and oxidative enzymes (Yost et al., 2010). However, the most significant effect might be disruption of coral reproductive processes. Concentrations at which reproductive effects occur vary with both metal type and coral species, but copper, zinc, nickel, lead, and cadmium have been shown to inhibit coral fertilization (Heyward, 1988; Reichelt-Brushett and Harrison, 1999; 2000; 2005) and nickel has been shown to cause mortality of larval and inhibit settlement (Goh, 1991).

While most heavy metal effects to corals are relatively chronic, effects to corals of petroleum products can be low-level chronic (drilling activities) or acute events (oil spills). There have been relatively comprehensive reviews of the effects of oiling on coral reefs (Knap et al., 1983; Loya and Rinkevich, 1980; Peters et al., 1997). As with most stressors, these effects have been context-dependent. Weathered oil is likely to be less injurious to coral reefs than fresh crude oil (Ballou et al., 1989), and vegetable oils are less toxic than mineral oils (Mercurio et al., 2004). Some studies show dispersants have little effect on corals, while others show that the effects of oil and dispersants combined are greater than either alone (Negri and Heyward, 2000) or that some dispersants are more toxic than others (Shafir et al., 2007). Drilling effects may be relatively confined (Hudson et al., 1982), but spills and seeps have more pervasive effects. Hydrocarbons produce a range of lethal and sublethal effects on corals that vary with severity of exposure. For example, oil concentrations were correlated with coral mortality in the Bahia las Minas event in Panama (Burns and Knap, 1989), and decreases in coral cover and diversity (Guzmán et al., 1991). Chronic oiling in the Red Sea increased mortality and reduced coral reproduction (Rinkevich and Loya, 1977), while short-term exposure or dispersed oil may show little residual effect on growth (Dodge et al., 1984). Corals have relatively high lipid content, which facilitates rapid uptake of hydrocarbons into coral tissues; but detoxification and depuration can be slow (Gassman and Kennedy, 1992; Kennedy et al., 1992; Solbakken et al., 1984). Exposure to drilling mud reduced calcification rates and protein concentrations in *Acropora cervicornis* (Kendall et al., 1983). In studies to date, oiling reduced photosynthesis, induced bleaching (Cook and Knap, 1983; Mercurio et al., 2004), and altered the lipid biochemistry of corals (Burns and Knap, 1989).

Oiling impaired gonad development in both brooding (Peters et al., 1981; Rinkevich and Loya, 1979a) and spawning corals (Guzmán and Holst, 1993). Crude oil inhibited metamorphosis (Te, 1991) and, to a lesser degree, fertilization (Negri and Heyward, 2000); some corals may abort reproduction by releasing planulae upon contact with oil (Loya and Rinkevich, 1979). Reproductive impairment has been exacerbated by the use of dispersants (Epstein et al., 2000; Negri and Heyward, 2000). Field surveys of chronically oiled sites suggest that coral recruitment and survival can also be impaired (Bak, 1987).

Pesticides and antifoulants are specifically engineered to induce mortality of invertebrates and enter coastal environments through terrestrial surface runoff and numerous boating activities, including being scraped off hulls during vessel groundings. Corals have been shown to bioaccumulate pesticides such as lindane, heptachlor, chlordane, and dichlorodiphenyltrichloroethane (DDT) (Glynn et al., 1989). Adult corals are usually not directly affected by herbicides (Peters et al., 1997); however, zooxanthellae have been shown to be affected at very low concentrations (ng/L) (Jones, 2005). Irgarol inhibited coral photosynthesis (Jones and Kerswell, 2003; Owen et al., 2002), while diuron was more toxic than atrazine (Jones et al., 2003) and 2,4-D (Råberg et al., 2003). Additionally, pesticides can significantly inhibit coral reproductive processes, inhibiting fertilization, settlement, and/or metamorphosis (Markey et al., 2007). High levels of diuron prohibited settlement of spawned, but not brooded, coral larvae; however, settled corals bleached and underwent polyp-bailout (Negri et al., 2005). Tributyl tin from ship hulls has been documented in coral reef areas (Inoue et al., 2004). Tributyl tin is not as toxic to fertilization as other heavy metals, but it has inhibited coral settlement and metamorphosis (Negri and Heyward, 2001; Negri et al., 2002).

In some coral reef areas, cyanide is used for fish collection. Cyanide exposure causes coral mortality, while sublethal effects include behavioral responses (polyp retraction, mucus expulsion), decreased zooxanthellae density, altered protein expression, tissue degradation, increased respiration, decreased photosynthesis, and bleaching (Cervino et al., 2003; Jones and Hoegh-Guldberg, 1999; Jones and Steven, 1997). Although the harmful effects of cyanide have come from direct application, low levels of accidentally introduced chemicals can also affect corals. For example, UV filters in sunscreens have promoted viral infection and induced coral bleaching when applied in very high concentrations (Danovaro et al., 2008). Endocrine disruptors from human sources have been documented in coral reef areas (Kawahata et al., 2004); such compounds have been shown to reduce coral growth and fecundity, and increase tissue thickness (Tarrant et al., 2004).

The general effects of contaminants on coral communities are reductions in coral growth, coral cover, and coral species richness (Keller and Jackson, 1991; Loya and Rinkevich, 1980; Pait et al., 2007) and a shift in community composition

to more tolerant species (Rachello-Dolmen and Cleary, 2007). Often, these changes are attributed to “pollution” or “contamination” so it is difficult to attribute changes to particular causes, particularly since toxins are often associated with other stresses, like sedimentation and runoff. It is also logical to assume that contaminants may have harmful effects in combinations that would not be evident by exposure to an individual substance. Furthermore, contaminant effects are species-specific. Bioaccumulation may be correlated with growth morphology and polyp size (Scott, 1990), and brooded coral larvae may be less exposed to contaminants than spawned gametes, which must fertilize and develop in the water column (Peters et al., 1997). While it is impossible at current levels of knowledge to quantitatively characterize and prioritize the level of threat that contaminants pose, the ability of contaminants to impair coral reproduction is not a negligible factor in locations where elevated toxins exist, particularly when other stresses are contributing to depensatory population effects. Furthermore, even if urban and industrial contaminants in coastal waters are each only local, recent findings suggest that they are fragmenting and isolating populations (Puritz and Toonen, 2011), which could limit connectivity and cause depensatory effects. Therefore, the BRT considers contaminants, despite their primarily local sources and direct impacts, to pose low, but not negligible, extinction risks to the 82 candidate coral species.

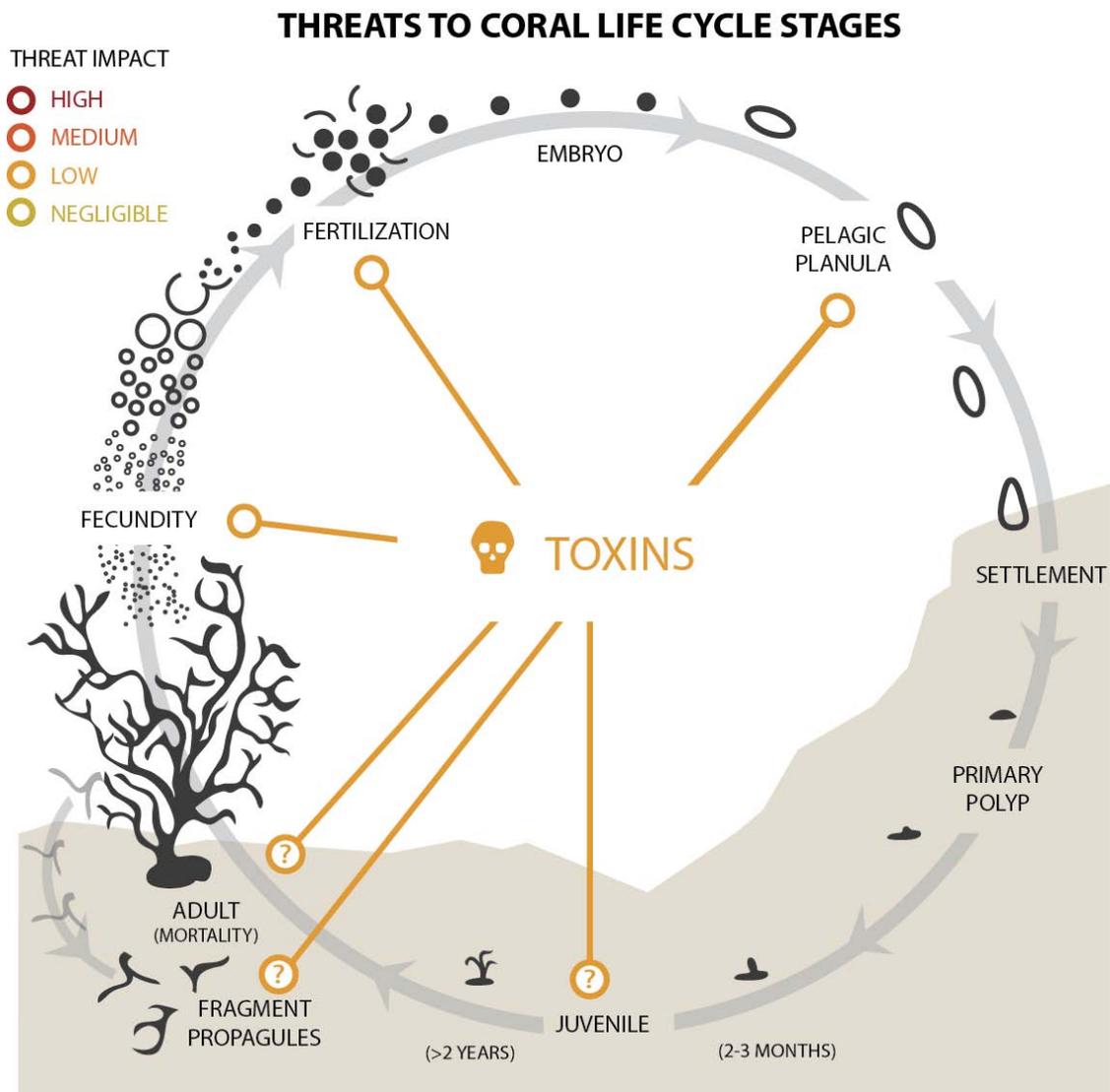


Figure 3.3.3. The impacts of toxins to various coral life history stages, including adult fecundity, fertilization, possibly adult mortality and fragmentation, and juvenile growth. The overall contribution of toxins to extinction risk for the 82 candidate coral species was determined to be **low** by the BRT. However, it is also clear that there is much to be learned about diffuse and combined effects of toxins and this assessment might require revision with improved future understanding. Diagram prepared by Amanda Toperoff, NOAA-PIFSC.

3.3.1.4 Salinity impacts

Many coral reefs are primarily influenced by open-ocean seawater conditions, creating relatively stable salinity conditions over the long term (Coles and Jokiel, 1992). Nevertheless, nearshore coastal corals can experience extreme salinity changes. Evaporation during extreme droughts and during windy, hot conditions on shallow banks can produce hypersaline waters (Kosaki, 1989; Porter et al., 1999), while hyposaline water is released into the coastal zone following heavy rain events (cyclones or monsoons) and can persist for several weeks or longer (Berkelmans and Willis, 1999; Lirman et al., 2003). For coastal reefs, rain events drive coastal runoff or groundwater inputs, both of which can bring other associated stresses (see above sections on nutrients, sediment, and toxins). Additionally, some corals inhabit what are essentially estuarine environments and must cope with tidally varying salinity changes. Coral responses to salinity are, in part, controlled by behaviors, such as polyp retraction and mucus production (Manzello and Lirman, 2003; Muthiga and Szmant, 1987) and osmoregulation via control of ions, free amino acids, glycerol, and osmotically active particles by the coral and its associated zooxanthellae (Mayfield and Gates, 2007).

High and low salinity can influence corals during many life stages (Fig. 3.3.4). Severe rain events can produce catastrophic local coral bleaching, but mortality may occur primarily in shallow depths (low salinity water is less dense, creating haloclines) and corals vary in their susceptibility to hyposaline events. For example, a single storm in 1987 reduced the salinity in parts of Kāneʻohe Bay, Hawaiʻi to 15 parts per thousand (ppt), causing mass mortality to *Pocillopora damicornis* and *Montipora verrucosa* at depths of ~ 2 m. *Cyphastrea ocellina* persisted, while *Fungia scutaria* and *Porites compressa* showed rapid tissue regeneration despite appearing dead (Jokiel et al., 1993). Similarly, Cyclone Joy and the wet season that followed it caused widespread mortality of reef organisms to depths of 1.3 m in the Keppel Islands on the Great Barrier Reef (windward reefs and those away from the Fitzroy River plume were unaffected). *Acropora* and pocilloporids suffered highest mortality; massive *Porites*, *Montipora*, and *Galaxea* partially bleached but recovered; *Leptastrea*, *Cyphastrea*, *Goniastrea*, and *Turbinaria* were among the least affected species (Van Woesik, 1991; Van Woesik et al., 1995). Nakano et al. (2009) observed a similar response in Thailand, where a 1995 flood did not affect massive *Porites* but primarily bleached *Pocillopora* and *Acropora*. Hyposaline water-induced bleaching following Hurricane Flora in Jamaica was greatest in *Millepora*, *Montastrea annularis* complex and *Manicina*, while *Siderastrea*, *Stephanocoenia*, and *Diploria* were the most resistant (Goreau, 1964).

These species-specific differences have also been reflected in sublethal responses. *Porites furcata* (Manzello and Lirman, 2003) and *Turbinaria reniformis* (Faxneld et al., 2010) maintained autotrophic capabilities (photosynthesis/respiration ratio > 1) in variable salinities, while photosynthesis/respiration ratios in *Porites lutea* were less affected by salinity than in *Pocillopora damicornis* (Moberg et al., 1997). *Montipora* and *Galaxea* bleached more easily at 17 ppt than *Porites* and *Platygyra* (Nakano et al., 2009), although only *Porites* showed no mortality. *Porites* in both the Atlantic and Pacific have tolerated salinity ranges of 20–45 ppt (Manzello and Lirman, 2003; Marcus and Thorhaug, 1981), while *Siderastrea* species in Florida have commonly been exposed to salinity extremes (10–37 ppt; Lirman and Manzello, 2009) and have acclimated to salinities as high as 42 ppt (Muthiga and Szmant, 1987).

A general response of corals to salinity decrease is the formation of mucus and tissue swelling (Coffroth, 1985; Downs et al., 2009; Van Woesik et al., 1995). Physiologically, low salinity has had little effect on respiration, but reduced photosynthesis (Alutoin et al., 2001; Downs et al., 2009; Kerswell and Jones, 2003; Lirman and Manzello, 2009; Moberg et al., 1997). Muthiga and Szmant (1987) found a salinity change of 10 ppt was necessary to induce respiration and photosynthetic changes in *Siderastrea siderea*. However, even small changes in salinity disrupted detoxification and endocrine pathways and induced oxidative stress in *Stylophora pistillata* (Downs et al., 2009). Histologically, hyposaline conditions induced cell lysis, degradation and loss of zooxanthellae, and gonad damage (Downs et al., 2009; Van Woesik et al., 1995). Hypersaline conditions can also stress corals. Periodic density cascading of hypersaline waters may exacerbate temperature-driven bleaching (Dennis and Wicklund, 1993). High salinity has also stimulated expression of carbonic anhydrase and oxidative enzymes such as thioredoxin (Edge et al., 2005). High salinity reduced photosynthesis, but not to the degree that low salinities have (Lirman and Manzello, 2009).

Low salinity reduces fertilization success of broadcast-spawned coral gametes (Richmond, 1993). The effect of low salinity was found to be highly nonlinear; a salinity reduction of 5 ppt caused developmental abnormalities in *Acropora millepora* larvae, while no fertilization at all occurred at salinities ≤ 28 ppt (Humphrey et al., 2008). Reduced salinity increased mobility and mortality of *Montastrea faveolata* planulae, reduced planktonic duration, reduced selectivity of settlement substrate, and reduced the size of settled planulae (Vermeij et al., 2006). Low salinities also reduced settlement and caused abnormal skeletal development in Pacific brooding corals, although *Pocillopora* was more sensitive than *Cyphastrea* (Edmondson, 1929; 1946).

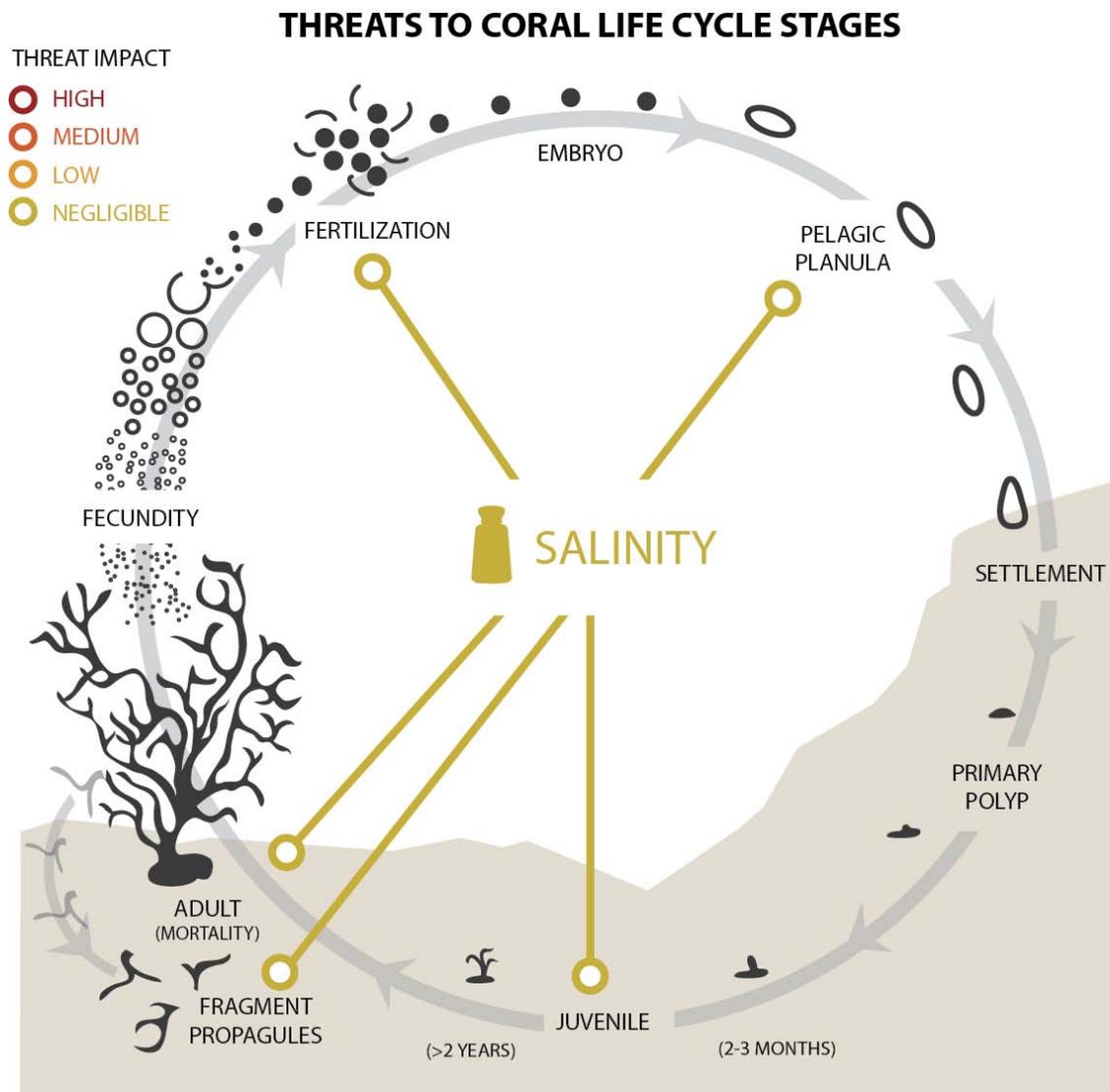


Figure 3.3.4. The impacts of salinity stress to various coral life history stages, including adult mortality and fragmentation, fertilization, pelagic planulae, and juvenile growth. The overall contribution of salinity stress to extinction risk for the 82 candidate coral species was determined to be **negligible** by the BRT. Diagram prepared by Amanda Toperoff, NOAA-PIFSC.

Most salinity stresses to corals are driven by rainfall, or the lack thereof. The short-term salinity tolerance range of corals is suggested to be 18–52 ppt (Coles and Jokiel, 1992). Short-term changes of less than 10 ppt are likely to have minimal or reversible effects (Hoegh-Guldberg and Smith, 1989a; Muthiga and Szmant, 1987). Climate change is expected to produce an increase in precipitation in many areas while reducing it in others. The general expected pattern is for wet areas/periods to become wetter, dry areas/periods to become drier, and precipitation to become more episodic (IPCC, 2007b). This would primarily be interpreted as a potential increase in the frequency and/or occurrence of hypersaline/hyposaline events. In some areas, coral spawning is cued by temperature changes from monsoon seasons (Ayre and Hughes, 2000; Guest et al., 2005b); increased rainfall during spawning could reduce coral reproduction. In coastal areas, increased rainfall could result in more runoff events with multiple stresses whose actions are difficult to predict. For example, the 1987 flood in Kāneʻohe Bay produced an additive effect; the freshwater kill was followed by a huge nutrient-driven phytoplankton bloom (Jokiel et al., 1993). Laboratory studies have documented the interaction of salinity with other stressors. *Turbinaria reniformis* tolerated low salinity and increased nitrate, but a temperature increase produced a synergistic effect, causing mortality in all cases (Faxneld et al., 2010). Similarly, low salinity reduced the ability of *Montipora verrucosa* to tolerate high temperatures (Coles and Jokiel, 1978). In contrast, effects can be antagonistic—low salinity and elevated copper both reduced photosynthesis in *Porites lutea*, but together they had no effect (Alutain et al., 2001).

Some evidence show that seawater salinity increased slightly in the Florida Keys from 1981 to 1988 as a result of evaporation (Halley et al., 1994). Extended droughts can produce salinities of 40–70 ppt in reef lagoons (Walton Smith, 1941), and corals exist in hypersaline waters in areas such as the Red Sea (Falkowski et al., 1984). Short-term meteorological events can produce pycnoclines, exposing the benthos to warm, hypersaline waters for several days to a few weeks (Kosaki, 1989). Hypersaline waters are undersaturated in aragonite and have been hypothesized to enhance dissolution of skeletal carbonates (Sun, 1992); if this applies to living corals as well it could exacerbate the effects of ocean acidification, but that remains to be tested. Given the spatial and temporal uncertainty in predicting weather and that remote reefs would be more likely to experience salinity changes in relative isolation (i.e., a reduction in other terrestrial runoff stressors), the BRT considered salinity effects to be a local and negligible overall contribution to extinction risk for the 82 candidate coral species.

The recent Reefs at Risk Revisited report (Burke et al., 2011) provided a global analysis of risk to coral reefs, by region and globally, to the impacts of watershed-based pollution (Fig. 3.3.5). While the watershed-based threats categorized in their analysis do not map perfectly with those discussed in the land-based sources of pollution threats section of this Status Review Report (Section 3.3.1), which included separation discussions about the threats to corals from sedimentation (Section 3.3.1.1), nutrients (Section 3.3.1.2), toxins and contaminants (Section 3.3.1.3), and salinity (Section 3.3.1.4), it is instructive to note the similarities of their independently derived analysis of these threats integrated together by region (Fig. 3.3.5).

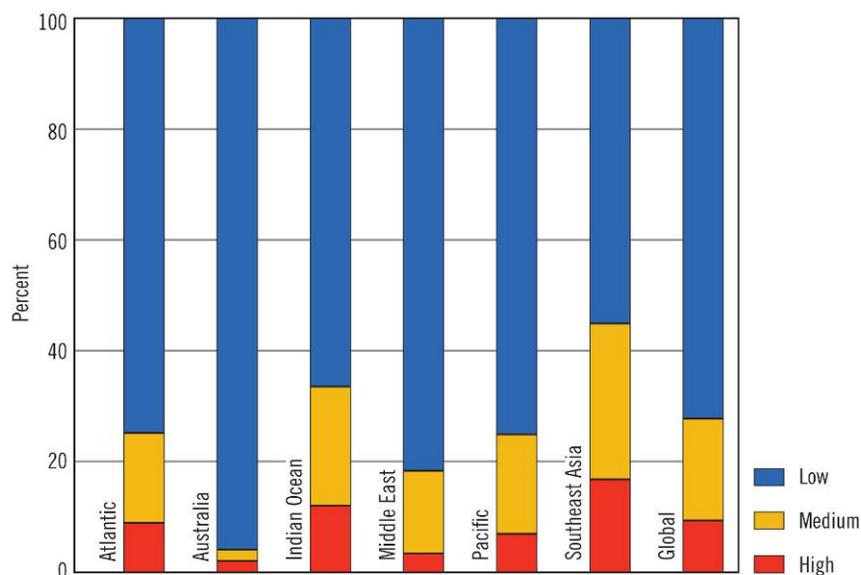


Figure 3.3.5. Global analysis of risk to coral reefs, by region and globally, to the impacts of watershed-based pollution. Risk was assessed through a GIS-based analysis of risk compiled from all available sources and categorized as low, medium or high threat to reefs in the region. For details on methods and a full description of threats included in this risk category, please see the original publication. From Reefs at Risk Revisited (Burke et al., 2011).

3.3.2 Disease

Disease is broadly defined as “any impairment that interferes with or modifies the performance of normal functions, including responses to environmental factors such as nutrition, toxicants, and climate; infectious agents; inherent or congenital defects, or combinations of these factors” (Wobeser, 1981). A disease state results from a complex interplay of factors including the cause or agent (e.g., a pathogen, an environmental toxicant, a genetic defect), the host, and the environment. In this case, the host is a complex holobiont that includes the coral animal, dinoflagellate, and microbial symbionts. For the purposes of this Status Review Report for the 82 candidate coral species, the effects that the BRT incorporates and ranks as “coral disease” are those characterized as presumed infectious diseases or those attributable to poorly-described autogenous malfunctions (e.g., genetic defects) and often associated with acute tissue loss. Other manifestations of broad-sense disease, such as coral bleaching or toxicological effects, are incorporated in other threat sections (e.g., toxins, acidification, warming).

Coral disease is a common and devastating threat affecting most or all coral species in various life stages (Fig. 3.3.6) and in all regions to some degree. For the most part, it is an “emergent” threat, not really recognized prior to the devastating effects on Caribbean *Acropora* spp. beginning in the early 1980s (Aronson and Precht, 2001; Bak and Crieens, 1982; Gladfelter, 1982; Porter, 1974). Since that time, rapid increases in the description of new diseases affecting corals, pervasive delirious outcomes throughout the Caribbean region, and growing recognition of impacts on corals in the Indo-Pacific basin have followed (Bruno et al., 2007; Galloway et al., 2009; Green and Bruckner, 2000; Harvell et al., 2007; Sutherland et al., 2004). At least two of the 82 candidate species (*Dichocoenia stokesi* and *Montastraea annularis* complex) have experienced documented dramatic, and likely unrecoverable, declines in local populations (up to 60% in one year) from disease, either alone or in conjunction with major bleaching events (Bruckner and Hill, 2009; Miller et al., 2009; Richardson and Voss, 2005).

The scientific understanding of disease etiology in corals remains very poor, despite more than over a decade of concentrated scientific attention (Richardson, 1998; Sutherland et al., 2004). However, some general patterns of biological susceptibility are beginning to emerge. Increased research attention to the processes of immunity in corals suggests that basic invertebrate mechanisms such as melanin-containing granular cells and phenoloxidase activity, are present and predictable patterns of basal immune capacity across coral families corresponding with trade-offs with other life history traits may exist (Table 3.3.1; Palmer et al., 2010). A recent meta-analysis by Diaz and Madin (2011) analyzed species-level disease occurrence on Australia’s Great Barrier Reef corals in relation to their ecological and biogeographic traits. They concluded that while many ecological factors were significantly correlated when examined alone, predator diversity, geographic range size, and characteristic local abundance were the most important collective predictors of disease potential (a measure of presence/absence, not severity) across coral species.

A primary question that remains poorly answered is: What is the contribution of local anthropogenic stressors (e.g., runoff or sewage) to increased coral disease impacts? A few correlative studies show significant local correlations with low water quality (Kaczmarzsky, 2006; Kaczmarzsky et al., 2005). Additional experimental studies suggest that more subtle aspects of local anthropogenic impacts may result in disease-like coral mortality. Smith et al. (2006) showed that experimental incubation of coral fragments with macroalgal thalli could result in coral mortality, which was, in turn preventable with the addition of antibiotics. These authors have suggested that leached organic matter from macroalgal biomass may trigger expanded microbial growth leading to coral mortality, and this effect might be an important factor in reefs that have undergone phase-shifts to high macroalgal standing stock. This possibility is consistent with results of Kline et al. (2006) showing that the experimental addition of organic carbon in lab tanks induced coral mortality while the addition of inorganic nutrients (nitrate, ammonia, phosphate) did not, and, consistent with Hodgson’s (1990) findings, tissue loss and mortality from sediment applications could be ascribed to microbial activity rather than the sediment per se. These studies point out the complicated trophic and ecosystem imbalances that are likely contributing to coral disease effects on modern coral reefs—simple explanations involving a single virulent pathogen do not appear likely.

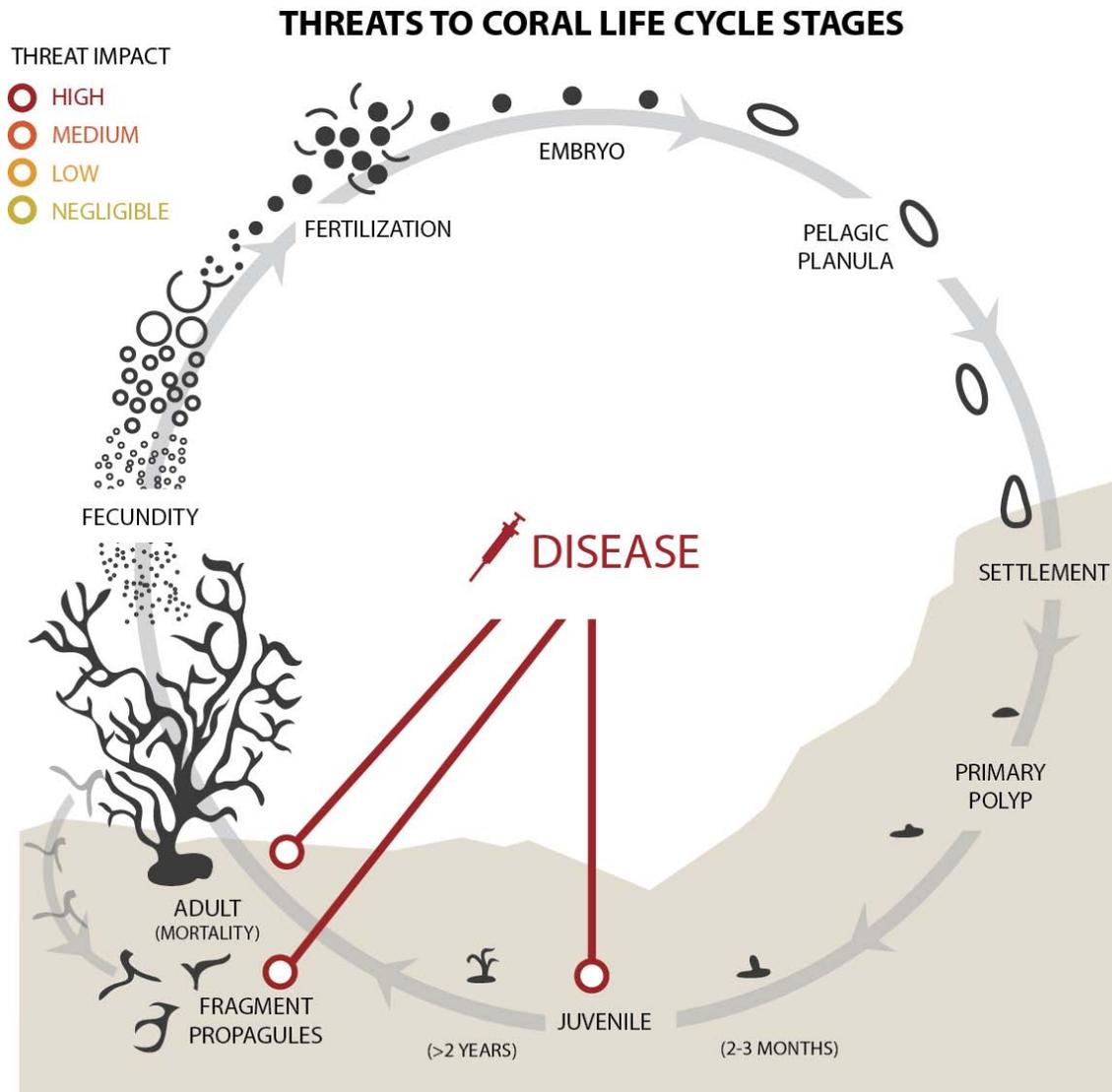


Figure 3.3.6. The impacts of disease to various coral life history stages, including adult mortality and fragmentation and juvenile growth. The overall contribution of disease to extinction risk for the 82 candidate coral species was determined to be **high-medium** by the BRT. Diagram prepared by Amanda Toperoff, NOAA-PIFSC.

In contrast, many examples showed no correlation between coral disease effects and local water quality (Jordan-Dahlgren et al., 2005) or that disease outbreaks occur in geographic areas remote from human population and land-based pollution (Aeby, 2005; Aronson and Precht, 2001; Bruckner and Hill, 2009; Miller et al., 2006a; Miller and Williams, 2007). Such patterns are consistent with increasing manifestation of diseases in both marine and terrestrial systems being linked with ocean warming climatic conditions (Harvell et al., 2002). Mounting evidence indicates that warming temperatures and coral bleaching responses are linked with increased coral disease prevalence, outbreaks, and mortality (Bruno et al., 2007; Jones et al., 2004; Maynard et al., 2010; McClanahan et al., 2009; Muller et al., 2008). Some coral diseases have been found to manifest peaks in prevalence and rate of progressions during summer periods of high temperatures (Boyett et al., 2007; Patterson et al., 2002; Sato et al., 2009), while others are influenced by more complex temperature patterns, including both winter and summer extremes (Heron et al., 2010). Increased temperatures may invoke increased virulence of pathogens, decreased resistance of hosts (e.g., Mydlarz et al., 2010; Ritchie, 2006) or both. In a related manner, the expanding coral disease threat has been suggested to result from opportunistic pathogens (i.e., ones that are not generally virulent) that become damaging only in situations where the host integrity is compromised by physiological stress and/or immune suppression (Lesser et al., 2007).

Table 3.3.1. Comparative immunity ranks and life-history traits compiled for seven scleractinian coral families. Table adapted from Palmer (2010). This ranking is consistent with the hypothesis that physiological investment in immunity represents trade-offs with investment in other life-history traits.

Family	Immunity Rank	Predominant Growth Form	Extension Rate	Reproductive Output
Acroporidae	Low	Branching	High	Intermediate/High
Pocilloporidae	Low	Branching	High	Intermediate/High
Faviidae	Intermediate/High	Massive	Intermediate/Low	Intermediate/High
Mussidae	Intermediate/High	Massive	Low	Intermediate/High
Fungiidae	High	Solitary	-	High
Poritidae	High	Massive	Low	Low

Coral diseases have already contributed to major population declines in many coral species in many locations, including some of the candidate species. Overall, disease represents a high-medium threat in terms of posing extinction risk to the 82 candidate coral species. The BRT understands from the best available information that the emerging disease threats most likely result from a combination of both local stressors and climate change. Coral disease outbreaks and substantial coral mortality have already resulted from disease effects directly linked to warm-temperature bleaching events. In some cases, such as the Caribbean *Montastraea* spp., widespread outbreaks of disease in combination with warming water temperatures and bleaching have already been manifested as a high threat, whereas disease is believed to represent a moderate but likely increasing threat (by 2100) to most of the other 82 species.

3.3.3 Predation

Predation on some coral genera, especially *Acropora*, *Montipora*, *Pocillopora*, and *Porites* in the Pacific and *Montastraea*, *Acropora* and some species of *Porites* in the Atlantic, by many corallivorous species of fish and invertebrates (e.g., snails and seastars) is a chronic, though occasionally acute, energy drain and threat to corals (Cole et al., 2008; Rotjan and Lewis, 2008) and has been identified for most coral life stages (Fig. 3.3.7). So far, 128 species of fish spread across 11 families have been found to prey on corals, with a third of the species relying on corals for more than 80% of their diet (Cole et al., 2008). In Hawai'i, Jayewardene et al. (2009) found 117 bites per m² on *Pocillopora*, 69 bites per m² on the branching *Porites compressa* and 4 bites per m² on the massive *Porites lobata*. Territorial corallivorous chaetodontids consume between 400 and 700 bites per hour from tabular *Acropora* (Gochfeld, 2004; Tricas, 1985). Corallivorous chaetodontids can be quite numerous, occurring at average densities of 50–70 fish per 1000 m². Unlike chaetodontids that eat polyps out of their calices, scarids remove significant amounts of skeleton as they feed. Individual adult bumphead parrotfish, *Bolbometopon muricatum*, have been estimated to remove 12.7–15 kg per m² of living coral skeleton per year (Bellwood et al., 2003). This has been calculated to be 2.3 m³ or approximately 5.7 metric tons of structural reef carbonate per year for each adult (Bellwood et al., 2003). Schools of *Bolbometopon* can consist of 30 to 50 fish or substantially larger and so a school of three or four dozen could remove up to 285 metric tons of reef framework per year over the area cruised by the school. In the Caribbean, a large population of parrotfishes (with most of the effect coming from *Sparisoma viride*) can remove 4 kg per m² per year (Bruggemann et al., 1994).

Several experimental field studies have demonstrated that the distribution of corals was directly limited by predation of corallivorous fishes and invertebrates (Grottoli-Everett and Wellington, 1997; Kosaki, 1989; Littler et al., 1989; Miller and Hay, 1998; Wellington, 1982). Predation of corals by fishes and invertebrates is normally considered negative, but triggerfish and pufferfish have been shown to disperse coral fragments during feeding, potentially helping corals spread by asexual reproduction (Guzmán, 1991). Some predators also affect the distribution of corals by preferentially consuming coral species or forms that are the faster growing and thereby superior competitors for space (e.g., *Acropora*, *Montipora*, *Pocillopora*, and branching *Porites*). For example, Cox (1986) found that by reducing the growth of the superior competitor (e.g., *Montipora capitata*), predators allow the more slowly growing coral (*Porites compressa*) to prevail.

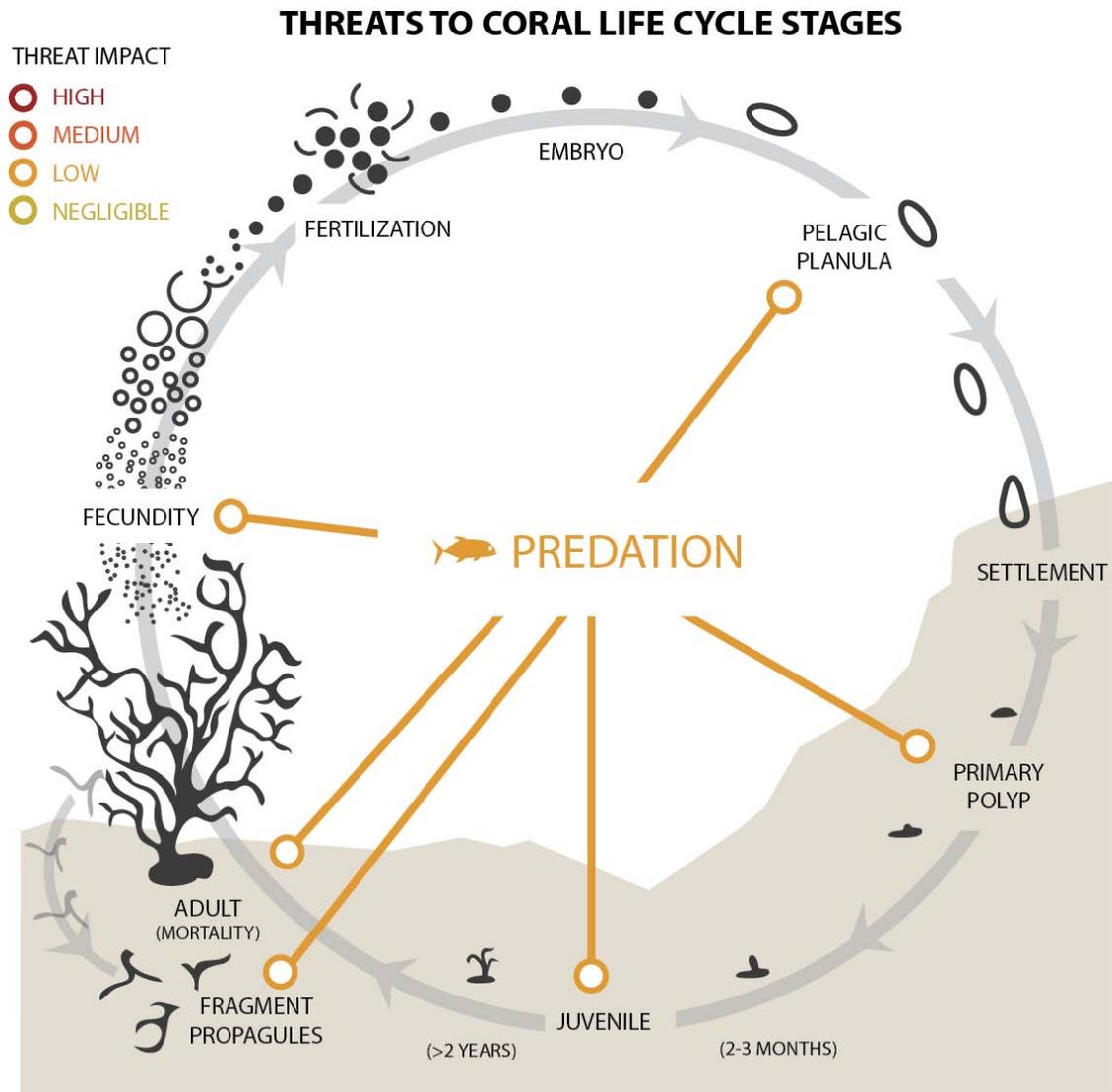


Figure 3.3.7. The impacts of predation stress by corallivorous fish and invertebrates to various coral life history stages, including adult mortality and fragmentation, pelagic planulae, polyp development, and juvenile growth. The overall contribution of predation stress to extinction risk for the 82 candidate coral species was determined to be **low** by the BRT. Diagram prepared by Amanda Toperoff, NOAA-PIFSC.

Large aggregations of crown-of-thorns seastars (*Acanthaster planci*), termed outbreaks, are among the most significant biological disturbances that occur on coral reefs (Moran, 1986). *Acanthaster planci* can reduce living coral cover to less than 1% during outbreaks (Birkeland and Lucas, 1990; Colgan, 1987), change coral community structure (Birkeland and Lucas, 1990; Branham et al., 1971; Pratchett, 2007), promote algal colonization (Moran, 1986; Moran et al., 1985), and affect fish population dynamics (Hart and Klumpp, 1996; Hart et al., 1996; Williams, 1986). The specific causative mechanisms that drive outbreak formation remain unknown with considerable debate about whether outbreaks in recent decades are more of a human-induced phenomenon as a result of sedimentation and urbanization (Brodie et al., 2005), runoff (Birkeland, 1982; Fabricius et al., 2010) or fishing (Dulvy et al., 2004) or primarily a naturally occurring phenomenon.

3.3.3.1 *Depensatory effects of predation*

In undisturbed conditions, the distribution of corals is affected by predation by fishes and invertebrates (Neudecker 1979; Wellington 1982; Cox 1986). Although observed distribution is often considered to represent the status quo, the realized niches of the affected corals may be only a minor fraction of what their fundamental niches and their realized niches might be in suboptimal environments. 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 the process of predation becomes depensatory, i.e., could produce positive-feedback effects, preventing the recovery of coral populations. Jayewardene et al. (2009) showed with field experiments that the effects of chronic and frequent predation on corals by fishes are usually inconsequential but become depensatory once the coral population decreases below a threshold (< 5% living cover in that study). Even with stable rates of coral predation, once a severe disturbance lowers the living coral cover below a threshold, predation by corallivorous invertebrates (Glynn, 1985b; Knowlton et al., 1990) or fishes (Guzmán and Robertson, 1989; McClanahan et al., 2005b; Rotjan et al., 2006) can hinder or even prevent the recovery of the coral populations. Once a coral population is severely reduced, populations of obligate corallivores might also eventually decline, thereby reducing predation pressure (Cole et al., 2008). Nevertheless, in the short term, fish and invertebrate obligate corallivore populations generally respond more slowly than the corals to the environmental stresses leading to predator concentration on reduced coral prey populations (Glynn, 1985a; Guzmán and Robertson, 1989; Knowlton et al., 1990). Predator concentration, in combination with the facultative corallivores, can accelerate the decline of stressed or disturbed coral communities as the ratio of predator to prey increases.

Eggs and larvae of corals are also intensely preyed upon by various reef fish species (Pratchett et al., 2001; Westneat and Resing, 1988). Several species of butterflyfishes (chaetodontid) prey on the larvae of *Heliopora coerulea* which are brooded on the surface of the colony (Villanueva and Edwards, 2010). *Heliopora coerulea* evolved around 130 Ma, but chaetodontid predators of coral larvae evolved less than 50 Ma (Bellwood et al., 2009) and *Heliopora coerulea* do not appear to have evolved adequate defenses. It has been suggested that this is possibly because no accidental mutational pathway for change in these corals which have large larvae and a solid colony skeleton has occurred. The large larvae are conspicuous, rich in energy with 41% dry weight lipid (Harii et al., 2007) and the butterflyfishes apparently take a serious toll on larval survival. However, as long as the reproductive population remains large enough, only a small portion of the brooded, benthic “crawl-away” larvae of *Heliopora coerulea* need to survive predation in order to maintain local populations.

Consumption of coral larvae in their pelagic stage is also a major trophic pathway (McCormick, 2003; Pratchett et al., 2001). Pratchett et al. (2001) reported 36 species of reef fish consuming coral propagules released during mass coral spawning. Stomach content analyses of three reef fish species (*Pomacentrus moluccensis*, *Abudefduf whiteyi*, and *Caesio cunning*) revealed that both *Pomacentrus moluccensis* and *Abudefduf whiteyi* feed almost exclusively on coral propagules during mass coral spawning, thereby providing direct evidence that reef fish benefit from mass coral spawning and revealing a potentially significant trophic link between scleractinian corals and reef fish. Although there has been a strong theoretical interest in establishing networks of marine protected areas to promote larval subsidies from upstream populations, recent quantitative field studies have shown that the larval supply is generally more local and self-seeding than theoretically predicted, despite the current speeds and the potential longevity of the larval stage in the life history (Warner and Cowen, 2002). Steneck (2006) explained how the size of the “dispersal kernel” or the distance over which larvae can subsidize downstream populations is determined by the effective population size of the source population. In theory, if predation on either the source population or the dispersing larvae reduces the number of coral recruits below a sustainable threshold, then predation becomes depensatory and positive feedback will propel the sink prey population towards local extirpation. That said, the arrival of even a few larvae over great distances may be important for reestablishment following local extirpation on a reef.

3.3.3.2 Synergistic effects of predation

Although the abundance of fresh bites by corallivorous fishes on the preferred corals is often impressive, these lesions usually heal. Healing time increases nonlinearly with lesion size (Van Woesik, 1998), but Jayewardene (2010) showed with laboratory experiments that regeneration of tissue over lesions was efficient and even very small fragments (1-cm tall) would heal without suppressing the growth of the coral. However, if healing is slowed by environmental stress, chronic predation can become the proximal cause of colony mortality (Jayewardene et al., 2009; Wellington, 1982).

In response to chronic and intense chaetodontid predation, coral polyps may remain withdrawn for long periods of time, and eventually the polyps can increase nematocyst density (Gochfeld, 2004). Hypothetically, both of these reactions can entail an energetic cost to the coral. It seems reasonable that as the coral populations decline and predation becomes more focused and intense, the energetic cost to the corals will become greater, healing of lesions might become slower, and the fecundity of the colony may be reduced. This interaction between concentration of predation and population size of the corals can become a positive feedback and depensatory once a threshold is crossed.

Important synergies of corallivory relate to the potential for coral predators to become vectors of disease transmission which could exacerbate mortality rates. A few experiments have demonstrated this potential for gastropod, polychaete, and fish corallivores (Aeby and Santavy, 2006; Nugues and Bak, 2009; Sussman et al., 2003; Williams and Miller, 2005). Anecdotal reports of corallivores preferentially targeting diseased tissue (Miller and Williams, 2007) emphasize that this phenomenon requires much further research.

3.3.3.3 *Outbreaks of predators*

Although predation is usually a chronic energy drain on corals (Jayewardene et al., 2009), acute massive outbreaks of some invertebrate corallivores can occasionally increase their population by up to 5 orders of magnitude in a single season. The gastropod *Drupella cornus* increased from 100 to 200 snails per km² of reef to 1–2 million per km² of reef and Ayling and Ayling (1987) calculated there were about 500 million *Drupella cornus* in Ningaloo Marine Park in western Australia. Birkeland and Lucas (2007) compiled reports on outbreaks of *Acanthaster planci*, with populations sometimes increasing within a few months from observations of about 10 per year to removal through a bounty system of greater than half a million per year. In some areas, such as the Great Barrier Reef, these outbreaks have commonly 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 abundant recruitment (Birkeland, 1982; Fabricius et al., 2010). Fishing on the predators of corallivores also has been suggested to contribute to these outbreaks. Recent increases in nutrient runoff, particularly input of fixed nitrogen into coastal waters from increased agricultural activities, coastal construction, and fishing on potential predators of corallivores are all contributing to changes on coral reefs. In some instances, these factors may be contributors to the recorded increases in the frequency of outbreaks of *Acanthaster planci*.

While chronic predation may structure communities and reduce the distribution of some of the preferred prey coral species (Gray, 1998; Grottoli-Everett and Wellington, 1997; Kosaki, 1989; Littler et al., 1989; Miller and Hay, 1998; Wellington, 1982), the less preferred coral prey are not as affected and their population prevalence might even be enhanced (Cox, 1986). During acute outbreaks, predators may feed more indiscriminately across coral species rather than focusing on preferred coral prey, sometimes nearly clearing living coral cover over large areas. The 1967 outbreak of *Acanthaster planci* around Guam depleted nearly all corals (except for a few *Diploastrea heliophora* and *Heliophora coerulea*) from 38 km along the west and northwest coast of the island (Chesher, 1969). The 1979 outbreak of *Acanthaster planci* around Palau cleared corals from 13 km² of reef habitat (Birkeland, 1982). It is reasonable to consider that the supply of coral planulae in the plankton might be spread too thin over such a large area to effectively reseed the reef (i.e., above the threshold of depensation discussed above), and so recovery might take decades or depend on an external supply of larvae. Even though these outbreaks are acute and local, if they become more frequent because of nutrient input, fishing or other factors, then their effects might accumulate over time because of the potential slow recovery. As these large areas accumulate, the decrease in supply of coral larvae and reduced topographic complexity could become depensatory factors on a large scale.

3.3.3.4 *Apex predators*

Corals are also thought to be indirectly affected by human removal of large apex predators. Reefs with larger predatory fishes may have large herbivore populations (Mumby et al., 2007b; 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 a trophic cascade effect of removal of top predators (see Section 3.3.4). Likewise, balistid, tetraodontid, and labrid fishes might control invertebrate corallivores such as gastropods (McClanahan, 1994) and *Acanthaster* (Dulvy et al., 2004). Therefore, apex predators are probably important for indirectly controlling macroalgae, which facilitates coral recruitment, and corallivores. Apex predators are often the prime targets of fishers and are easily depleted from coral reef ecosystems. Hence, they are now generally common only around remote Pacific islands and atolls where fishing pressure is slight (Sandin et al., 2008; Stevenson et al., 2007; Williams et al. 2011) and, possibly, also in other remote areas of the Indian Ocean and near Papua New Guinea.

Although large populations of herbivores are generally considered good for coral recruitment, the experimental results of Miller and Hay (1998) indicated that in some areas, herbivores can consume corals as well, to the extent of limiting the distribution of some species of corals and determining coral community structure (Sammarco, 1980).

3.3.3.5 *Summary of predation threats*

Predation on corals is normally chronic and frequent, thereby affecting the distribution of corals. Assuming the usual community structure of corals as the status quo, then the effects of predation on corals can be considered inconsequential. However, if outbreaks of corallivores or some other large-scale disturbances occur, such as cyclones,

disease or bleaching, by which the living coral cover is decreased below a threshold, predation can have positive feedback or compensatory effects in which the impacts of predation increase exponentially and inversely to the population density of the coral. This can prevent recovery or increase extinction risk. The increased focus of predation on the fewer remaining colonies can energetically cost the coral in defensive reactions and could result in a reduced rate of healing and/or fecundity or reduced resistance to stressors and/or disease. As human population densities increase in coral reef regions, it is almost certain that fishing pressures will likewise increase and that nutrient runoff into coastal waters will increase with land being cleared of native vegetation for agricultural or urban development. Nutrient runoff from land stimulates phytoplankton blooms which provide food for the larvae of invertebrate corallivores and facilitate abundant recruitment of corallivores and so can cause outbreaks of these predators (Birkeland, 1982; Fabricius et al., 2010). Fishing on the predators of corallivores may also contribute to outbreaks. As predation on corals becomes more frequent, the decrease in coral reproductive stock and larval production and the reduced topographic complexity could become compensatory factors on a large scale. Taking into consideration each of these direct and indirect effects of predation, which predominantly occur over local to regional scales, the BRT considered the overall global extinction risk posed by predation to be low.

3.3.4 Reef fishing—trophic cascades

Fundamental differences in ecosystem-level processes between coral reef and pelagic fisheries are evident. Oceanographic processes, such as wind-driven vertical mixing or equatorial upwelling of nutrients (i.e., “bottom-up”), are often the key driving forces in open-ocean pelagic ecosystems, while species interactions such as predation (i.e., “top-down”) are often the major controlling factors in coral-reef ecosystems. Fishing does not influence the process of upwelling, but on coral reefs, fishing or use of destructive fishing practices, can have large-scale, long-term ecosystem-level effects that can change ecosystem structure (“phase shifts”). Removal of biomass from coral reef systems by fishing alters trophic interactions that are particularly important in structuring coral reef ecosystems (e.g., Dulvy et al., 2004). Evidence from certain geographic locations shows that removal of fishing pressure in marine no-take reserves can lead to increased coral recruitment (e.g., the Bahamas, Mumby et al., 2007a).

Fisheries management strategies for coral reef ecosystems often include efforts to maintain resilience by trying to sustain populations of herbivorous fish, especially the larger scarine herbivorous wrasses, including parrotfish. On topographically complex reefs, population densities can average well over a million herbivorous fishes per km² and standing stocks can reach 45 metric tons per km² (Williams and Hatcher, 1983). In the Caribbean, parrotfishes can graze at rates of over 150,000 bites per m² per day (Carpenter, 1986) and thereby remove up to 90%–100% of the daily primary production of the reefs (Hatcher, 1997). Under these conditions of topographic complexity with substantial populations of herbivorous fishes, as long as the cover of living coral is high and resistant to being affected by environmental changes, it is very unlikely that the algae will take over and dominate the substratum.

When herbivorous fish populations are reduced but adult coral colonies maintain their resistance to physiological damage by climate change and human activities, coral-reef communities can persist. However, if herbivorous fish populations are heavily fished and high mortality of coral colonies occurs, then algae can grow rapidly and inhibit the replenishment of coral populations. Ecosystems can then shift into an alternative stable state (Mumby et al., 2007b). Although algae can have negative effects on adult coral colonies, the ecosystem-level effects of algae are primarily to inhibit coral recruitment (Fig. 3.3.8). Filamentous algae can prevent the colonization of the substratum by planula larvae by creating sediment traps that obstruct access to hard substrata for attachment. Macroalgae can suppress the successful colonization of the substratum by corals through occupation of the available space, by shading, abrasion, chemical poisoning (Rasher and Hay, 2010), and infection with bacterial disease (Nugues et al., 2004b).

With the increased scale and ubiquity of stress on adult coral colonies by human activities, e.g., ocean warming, acidification, sedimentation, anchor damage, trampling, dynamiting and other harmful fishing practices, etc., efforts to maintain population levels of herbivorous reef fishes as a strategy to enhance coral population replenishment have been increasingly important and challenging. There is often a strong cultural motivation in modern society to seek and catch the largest fishes. For parrotfishes, the effect of grazing by individuals > 20 cm in length is substantially greater than that of smaller fish (Bruggemann et al., 1996; Ong and Holland, 2010). Up to 75 individual parrotfishes with lengths of about 15 cm are needed to have the same effect on reducing algae and promoting coral recruitment as a single individual 35 cm in length (Lokrantz et al., 2008). Species richness of the herbivorous fish population is also necessary to enhance coral populations. Because of differences in their feeding behaviors, several species of herbivorous fishes with complementary feeding behaviors can have a substantially greater positive effect than a similar biomass of a single species on reducing the standing stock of macroalgae, of increasing the cover of crustose coralline algae (which

facilitates coral recruitment), and increasing live coral cover (Burkepile and Hay, 2008; Russell, 1992). Even if grazing pressure is relatively constant, the species responsible for algal removal may vary temporally (Wellington, 1982). In an ecosystem approaches to fisheries management sense, one strategy to sustain resilient coral communities would be to protect large individuals of multiple species of herbivorous fishes. To a limited degree, coral reefs can compensate for the removal of herbivorous fish by an increase in other herbivorous organisms. For example, reefs in Jamaica remained high-coral, low-algal systems despite high fishing pressure because of the extremely high abundance of grazing *Diadema* urchins, but became macroalgal dominated after the 1983 die-off of *Diadema* (Hughes, 1994 and references therein).

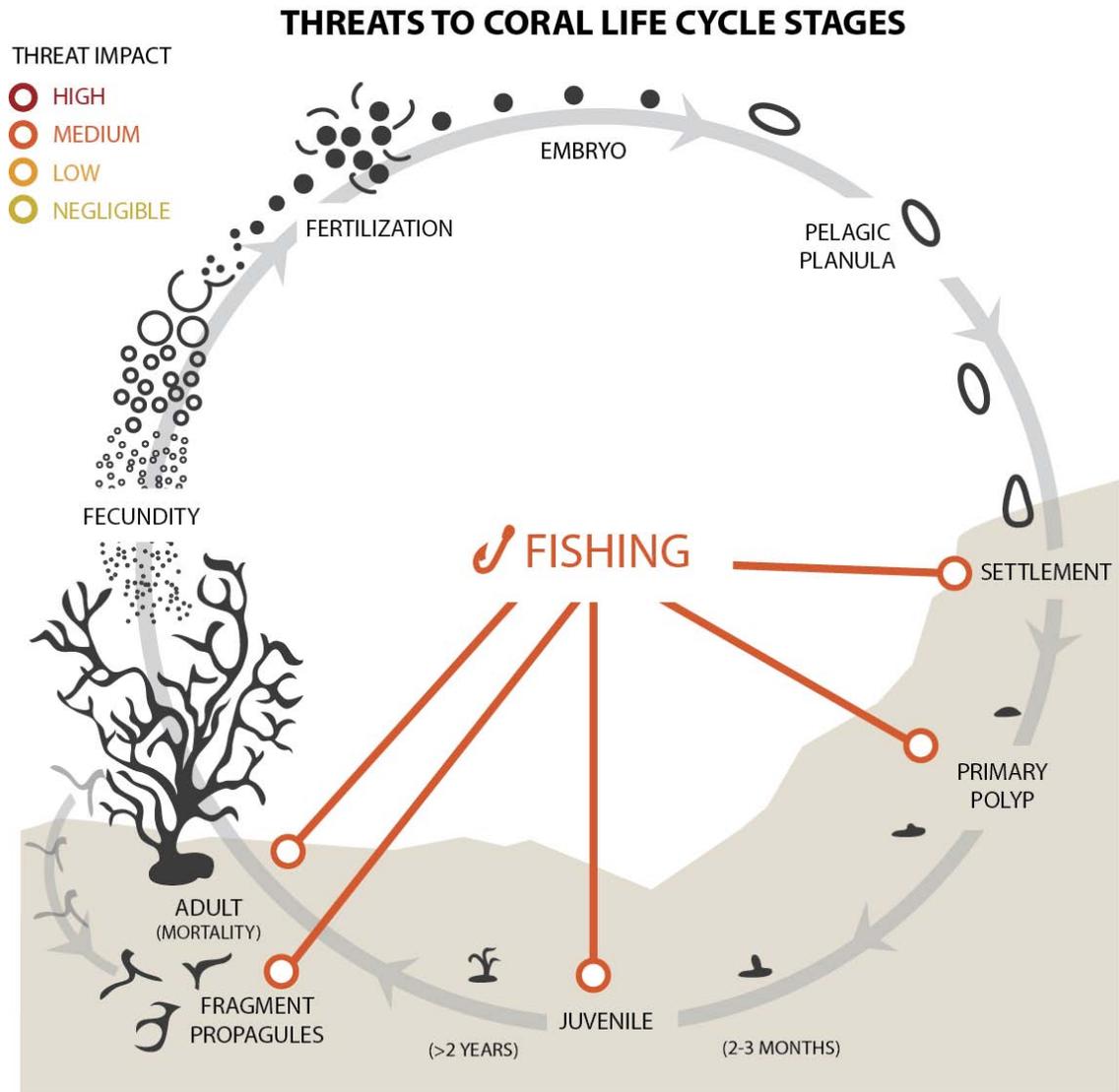


Figure 3.3.8. The impacts of fishing stress (fishing or destructive fishing practices) to various coral life history stages, including adult mortality and fragmentation, settlement, polyp development, and juvenile growth, many of which are via indirect effects on trophic cascades and habitat structure. The overall contribution of fishing stress to extinction risk for the 82 candidate coral species was determined to be **medium** by the BRT. Diagram prepared by Amanda Toperoff, NOAA-PIFSC.

Fishing also can have further consequences on coral mortality via trophic cascades. Corallivores may be released from population control by predation when their predators are reduced by fishing (e.g., Burkepile and Hay, 2007). In addition, Raymundo and colleagues (2009) found significantly lower frequency of coral disease in fishery reserves than in adjacent unprotected reefs across seven marine reserves in the Philippines. They also reported that coral disease prevalence was negatively correlated with several parameters of reef fish diversity across these sites and positively correlated with chaetodontid abundance. Hence, retaining functionally-diverse reef fish communities was closely linked

with improved coral health in that study and are consistent with the hypothesis that corallivorous chaetodontids are released from predation by targeted fishes outside of reserves, yielding increased transmission of disease from one coral colony to another as they move around and take bites from each coral colony as suggested by Aeby and Santavy (2006).

The ultimate drivers of increased fishing on coral reefs in both tropical developing countries and wealthy tropical and subtropical countries are increases in human population densities and per capita net consumption. In less developed tropical countries, increases in tropical human population densities are greatest in the coastal regions. The rate of destructive effects to coral reefs by reef fisheries can exceed the rate of human population growth because the number of job opportunities per capita and the amount of open farmland and other terrestrial resources substantially decreases with tropical coastal population growth. As terrestrial resources become overutilized, coastal fringing reefs become “welfare resources” (McManus, 1997; McManus et al., 1992). People naturally turn towards near shore fishing because reefs represent “easy entry” resources as traditional fishing rights break down. Compared to starting a livelihood or obtaining food for families in heavily-populated coastal land areas, very little capital investment is required for people to gather shells by hand or fish with a handline from a bamboo raft (McManus, 1997; McManus et al., 1992).

In more developed and wealthy countries, fishing down the food web and modifying the trophic structure of reef communities is also a direct result of the increase in human population densities (Williams et al., 2008c). For example, Hawai‘i has more than 260,000 recreational fishers (<http://hawaii.gov/dlnr/dar/hmrfs.html>) and fishing has reduced the density of apex predators in the populated main Hawaiian Islands to about 3% of levels in the uninhabited and relatively unfished shallow reefs of the Northwestern Hawaiian Islands (Friedlander and DeMartini, 2002; Williams et al., 2011). In the Florida Keys, more than 50,000 recreational fishers were reported to have reduced populations of spiny lobster (*Panulirus argus*) by 80%–90% in the 2-day sport season (Eggleston et al., 2008).

3.3.5 Direct habitat impacts and destructive fishing practices

Fishing activities also have direct impacts on coral colonies and habitats when various gear or fishing practices interact directly with reef substrates. While the effects of fish removal are largely reversible on decadal or shorter time scales (as evidenced by growing literature on recovery in many fisheries reserves), habitat degradation, particularly loss of three-dimensional architectural structure, is a much more potent threat to long-term recovery of reef fish stocks (De Putron et al., 2010; Fox et al., 2003; Syms and Jones, 2000). Both active and derelict fishing gear can destroy benthic structure and habitats, kill reef-building organisms, and entangle benthic and mobile fauna, including endangered species (Donohue et al., 2001). As an example of the amounts of derelict fishing gear affecting coral reefs, Dameron et al. (2007) estimated that at least 52 metric tons of derelict fishing gear recruit each year from distant fisheries (thousands of kilometers away) and become entangled on reefs of the remote Northwestern Hawaiian Islands. Various ecological effects occur when traps and bottom trawls are deployed, but deleterious effects may also occur when large numbers of anglers use hook-and-line gear to fish (Jennings and Lock, 1996). Trawls dislodge and abrade corals, while stationary gear such as traps damage corals and other sessile fauna via movement during even mild storm events (Lewis et al., 2009) and during gear retrieval in adverse conditions. Storms can mobilize traps and cause buoy lines to snare branching corals.

Fishers in some parts of the world employ explosives or toxic chemicals such as sodium hypochlorite and sodium cyanide to harvest fish and invertebrates (Campbell, 1977; Edinger et al., 1998; McManus, 1997). These practices, well-known in parts of Southeast Asia and the western Pacific, are not as well documented in Caribbean waters. The consequences of these practices to corals are described in Sections 3.3.1.3 and 3.3.6. Dynamite blast fishing disturbs extant colonies while destroying reef frameworks, slowing recovery of coral populations in these areas (Fox et al., 2003).

In contrast to earlier days when fishing gear represented a substantial investment, technological advances have provided humans with the ability to manufacture traps, monofilament gill nets, larger nets and fishing lines inexpensively. The modern, efficient production of these devices makes them essentially disposable; they can be abandoned if retrieving them becomes overly time-consuming or expensive. Abandoned synthetic fishing gear can continue “ghost fishing” or habitat destruction for decades. The decreased manufacturing cost and efficient rapid production, in combination with the increased longevity of the synthetic materials in the ocean (i.e., technology), lead to an increasing accumulation of materials that abrade and dislodge corals. The increasing demand for protein by growing human populations has accelerated the production of synthetic fishing gear and accumulation of derelict gear, resulting impacts to coral reefs. While effects of destructive fishing practices can be locally severe, the BRT considered their overall contribution to global extinction risk to the 82 candidate coral species to be low.

The recent Reefs at Risk Revisited report (Burke et al., 2011) provided a global analysis of risk to coral reefs, by region and globally, to the impacts of fishing and destructive fishing practices (Fig. 3.3.9). While the threats posed by fishing and destructive fishing categorized in that report do not map perfectly with those discussed here in the sections on Reef fishing—trophic cascades (3.3.4) or on Direct habitat impacts and destructive fishing practices (3.3.5), the analysis of these threats by region is similar (Fig. 3.3.9).

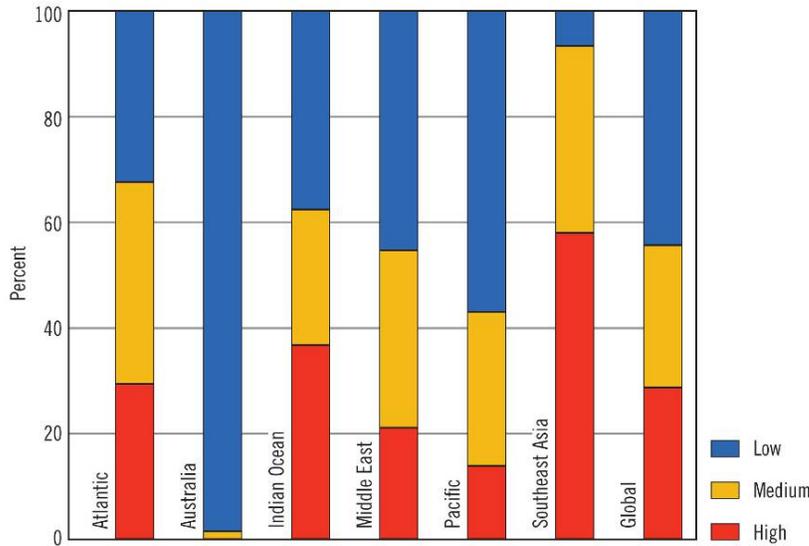


Figure 3.3.9. Global analysis of risk to coral reefs, by region and globally, posed by fishing and destructive fishing practices. Risk was assessed through a GIS-based analysis of risk compiled from all available sources and categorized as low, medium or high threat to reefs in the region. For details on methods and a full description of threats included in this risk category, please see the original publication. From Reefs at Risk Revisited (Burke et al., 2011).

3.3.6 Ornamental trade

Ornamental trade of various kinds removes or destroys adult and juvenile reef corals (Fig. 3.3.10). Globally, 1.5 million live stony coral colonies are reported to be collected from at least 45 countries each year. Of these, the United States is the largest consumer of live corals (64%) and live rock (95%) for the aquarium trade (Ruiz et al., 1999; Tissot et al., 2010). The imports of live corals taken directly from coral reefs (not from aquaculture) increased by 600% between 1988 and 2007, while the global trade in live coral increased by nearly 1500% (CITES, 2010; Tissot et al., 2010). It is estimated that 30 to 50 metric tons of red and black corals, and 2000 metric tons of stony corals, are exported each year within the ornamental trade (CITES, 2010; Tissot et al., 2010). Much of the harvest of stony corals is highly destructive, removing and discarding large amounts of live coral that go unsold and damaging reef habitats around live corals. The result is destruction of much more coral and reef area than that which is exported (Bruckner et al., 2001).

Globally, it is estimated that the number of aquarium fishes taken from coral reefs is about 20 times the number of live corals taken (Tissot et al. 2010). As an illustrative example of increases in the aquarium trade, the number of coral-reef fishes collected from just the leeward coast of Hawai'i Island for the aquarium trade increased from 90,000 in 1973 to 422,823 in 1995 (Tissot and Hallacher, 2003). It should be noted that the collection of reef fishes and/or invertebrates can be as harmful to corals and coral-reef structures as the collection of corals directly if destructive methods are used. From the reefs of Kāne'ohe Bay, Hawai'i, the average number of feather-duster worms (*Sabellastarte sanctijosephi*) collected per year for the aquarium trade was reported to be 43,143 (Friedlander et al., 2008). As each feather duster worm is obtained by breaking away the coral, the total coral and habitat damage can be significant. Although illegal, cyanide continues to be used in many parts of the Indo-Pacific for collecting reef fishes. According to the World Wildlife Fund, six thousand divers in the tropical Pacific inject an estimated 150,000 kg of sodium cyanide onto about 33 million coral heads each year, although this includes the food fish trade as well as the aquarium trade. According to three precautionary estimates, the reef-degrading capacity of the cyanide fishery for food fish on Indonesia's coral reefs amounts to a loss of live coral cover of 0.047, 0.052 and 0.060 m² per 100 m² of reef per year (Mous et al., 2000). Sodium cyanide can cause bleaching and mortality in corals (Jones and Steven, 1997). In addition to these direct impacts of aquarium trade removals, there are mounting concerns, given the exponential growth in the total market, of

potential trophic cascade effects from loss of small invertebrates whose ecological functions within the reef community remain inadequately characterized (Rhyne et al., 2009).

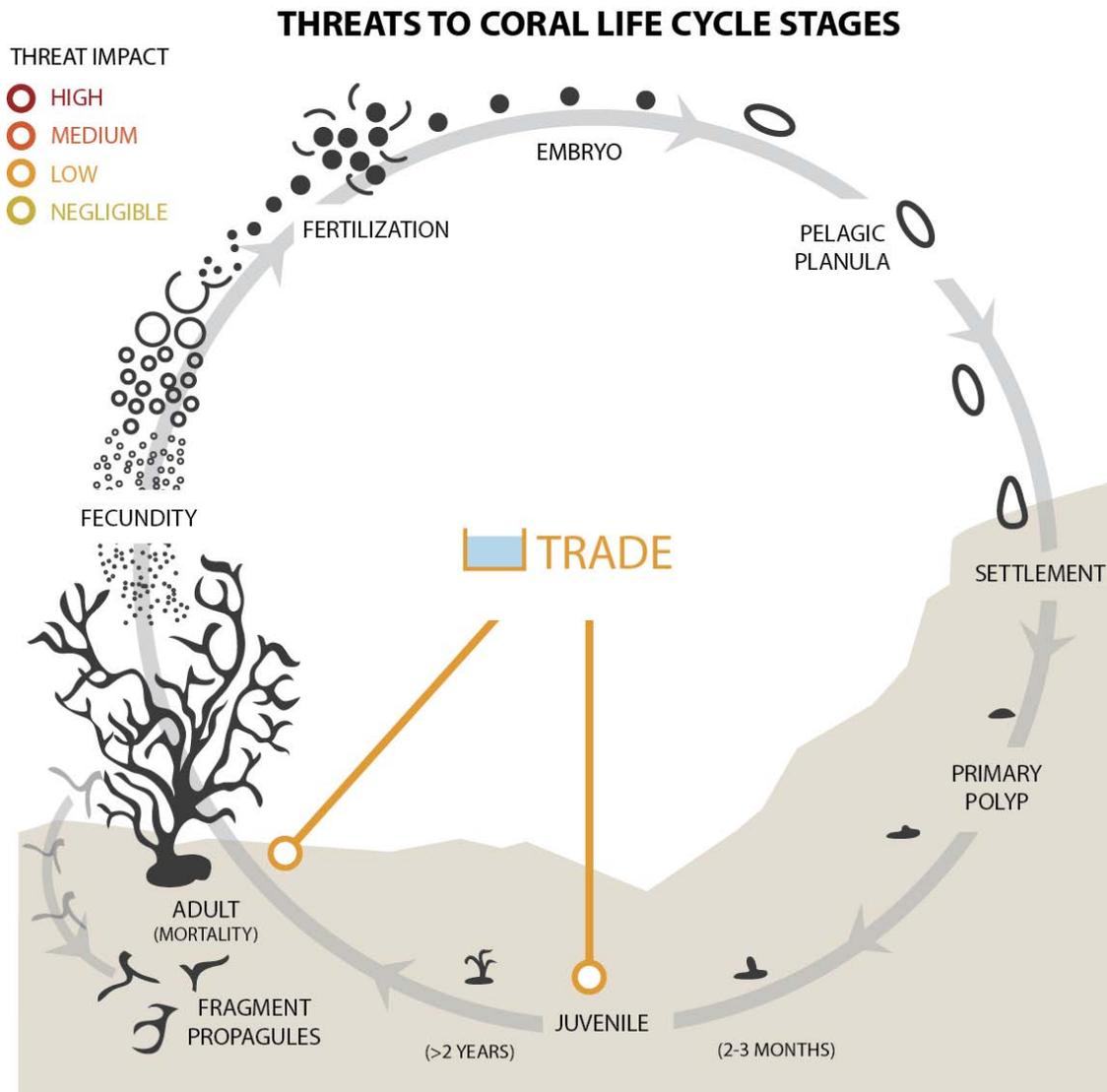


Figure 3.3.10. The impacts of ornamental trade to various coral life history stages, including adult mortality and juvenile growth. The overall contribution of ornamental trade to extinction risk for the 82 candidate coral species was determined to be **low** by the BRT. Diagram prepared by Amanda Toperoff, NOAA-PIFSC.

Since stony corals are predominantly sessile and most are externally fertilized (~ 75%), sustainability of spawning populations depends partly on maintaining sufficient colony densities to ensure that gamete dilution is not too great to support successful external fertilization. Although brooders have internal fertilization, sperm can be diluted in the water column for non-hermatypic species. There may be thousands of colonies of a particular species in an archipelago, but as their density is reduced by collection (as with any other source of adult mortality), the chances of successful fertilization and successful larval production decline (Coma and Lasker, 1997; Levitan et al., 2004), perhaps to some threshold level which has not been quantified. There have not been sufficient studies to date to determine these threshold levels definitively, but preliminary studies have suggested that threshold distances are probably in the general range of 10 m (Coma and Lasker, 1997; Lacks, 2000). We cannot dismiss the possibility that when dilution substantially decreases the probability of fertilization, the occasional larva might be insufficient for replenishing the population subjected to the occasional threats of predation, competition, and the aquarium trade. For example, *Heliopora coerulea* have crawl-away brooded larvae. The local communities can replenish themselves if they have local reproductive stock, but they cannot

replenish themselves from distant populations kilometers away—so it is especially important that the collectors in the aquarium trade leave colonies in close proximity.

The economics of the collection of marine fauna for luxury items, such as aquaria and ornaments, involves a detrimental positive feedback in that the more rare an item becomes, the more valuable and intensively collected it becomes. Some jurisdictions, such as Fiji, have apparently harvested for the aquarium trade those corals most sustainable and not harvested more vulnerable species, such as *Heliopora coerulea*. Commercial interest in coral harvest was high enough that several papers in the 1980s applied traditional fishery-based sustainable harvest models to evaluate the potential maximum sustainable yield for coral populations (Grigg, 1984; Ross, 1984). More recent work has focused on consumptive pressures (Tissot et al., 2010) and sustainable practices (Harriott, 2003).

Enforcement of rules in the aquarium trade is not easy because of difficulty with species identification of corals. The websites of the aquarium trade often have misidentified photographs, and species that are difficult to distinguish are often reported at the genus level. This makes it problematic to accurately track the species that are traded and even more difficult to understand the potential population-level effects of collections. The tracking issues are sufficiently confused that there have been reports of active trade in specimens of both extinct genera and those collected from exceptionally deep waters (80–2300 m) that are outside the range of typical collection practices (Green and Shirley, 1999). Monitoring transshipment is an additional problem. Ornamental coral (live and dead) and fish may be shipped from one country to another for declaration, increasing errors in tracking trade and in estimating effects on wild populations.

Over the past few decades trade has focused increasingly on live coral specimens for recreational aquaria rather than for jewelry or other ornamental uses (Green and Shirley, 1999). Because of difficulties in tracking and enforcement, concerns are often raised that permitting the export of cultured dead or live corals may increase pressure on the trade in non-cultured corals. Collection of some coral reef animals for trade has caused virtual extirpation of local populations, major changes in age structure, and promotion of collection practices that destroy reef habitats (Tissot et al., 2010). Most often, this is the case for reef-associated organisms (fish, cryptic invertebrates, etc.), but documented declines to reef corals themselves also occur. For example, surveys in the Philippines showed significant decreases in the abundance and colony size of targeted coral species; this was particularly problematic in that the size of corals targeted for collection was smaller than the minimum reproductive size for several of the species of interest (Ross, 1984). Overall, collection for the coral trade can have significant local effects on reefs as a whole and targeted coral species in particular. However, these effects are minor compared to those from land-based pollution, fishing, and climate change (Green and Shirley, 1999). The BRT concurred and assumed coral trade to be a low extinction risk in this evaluation.

3.3.7 Natural physical damage

Coral reefs must endure physical damage from many different sources and threats acting over a range of spatial and temporal scales. Extreme wave events, such as those generated by severe tropical or extratropical cyclones and tsunamis, are naturally occurring processes that are typically viewed as acute disturbances. Direct physical effects from vessel groundings and coastal construction activities, such as dredging, mining, and drilling, are somewhat analogous to storm damage in that they are relatively discrete events, although they generally occur over much smaller spatial scales than do storms or tsunamis. Other human-induced disturbances, such as those caused by tourism and recreational events and marine debris, can have pervasive, chronic physical consequences. The relationships between injury interval and time required for reef recovery are the primary factors in evaluating equilibrium of the system (Connell, 1978).

The frequency and intensity of storms are projected to change with climate change (see Section 3.2.6). Severe storms are often major stressors to reef systems, but their effects tend to occur over relatively local to regional scales and they are likely to have relatively little importance in terms of extinction risk. For the purposes of this Status Review Report, the BRT considered storm events to have the potential to significantly reshape the zonation of coral communities at a local scale, particularly when storms return at frequent intervals. However, the effects of tropical cyclones are generally dwarfed by the outcomes of other stressors acting over larger spatial scales and longer temporal scales (Gardner et al., 2005). While the BRT recognizes that these physical impacts can have significant effects on species with limited geographic ranges or contribute to local extirpations of widespread species, the overall contribution to extinction risk is considered low and primarily acts on life stages from settlement to adulthood (Fig. 3.3.11).

Prevailing hydrodynamic regimes (waves, currents, tides) are critical in determining coral colony morphology and benthic community composition (Kaandorp, 1999; Storlazzi et al., 2005). Partial mortality of coral colonies increases their vulnerability to bioerosion (Scoffin et al., 1997), which increases the porosity of coral skeletons and makes them

more prone to breakage (Chamberlain, 1978). The relationship between seasonal wave energy and coral skeletal strength controls the spatial zonation of coral reefs, particularly the distribution of species (Graus and Macintyre, 1989; Storlazzi et al., 2005). Substrate strength can be a greater contributor to breakage than colony strength per se (Madin, 2005), and colony morphology has a significant effect on whether colonies become dislodged (Madin and Connolly, 2006). Dislodged or fragmented colonies that are loose generally incur mortality (Woodley et al., 1981) or become projectiles that inflict further damage to the reef (Massel and Done, 1993)—while colonies that reattach to the substrate can contribute to coral population as asexual “recruits” (Highsmith, 1982). Preliminary stabilization of loose fragments and other rubble is accomplished by reductions in wave energy and biological growth, while rigid binding is accomplished by cementation and calcifying marine organisms (Rasser and Riegl, 2002). If conditions are favorable and species are fast-growing, coral fragments can begin to stabilize within a few weeks of a storm (Glynn et al., 1998).

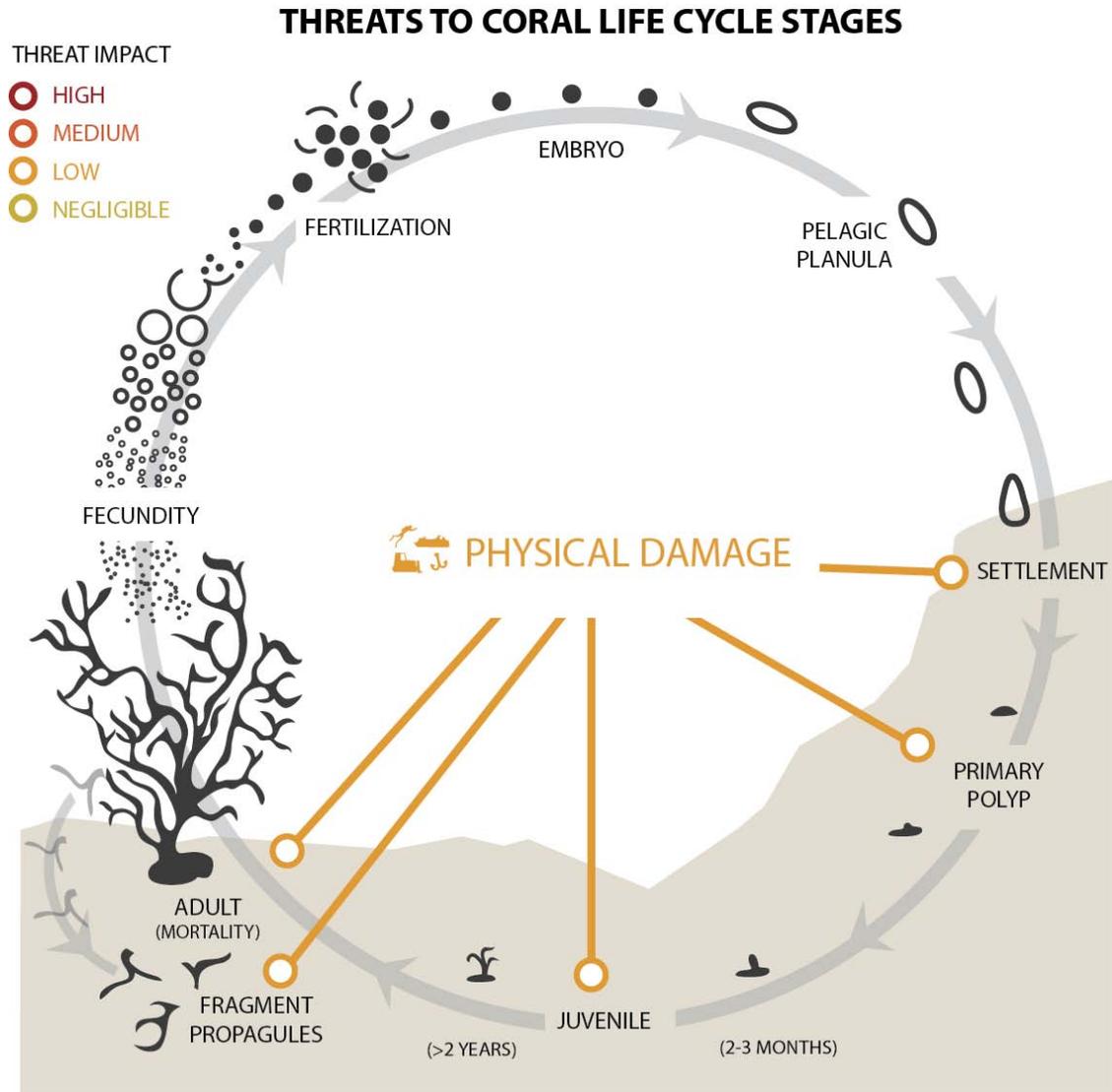


Figure 3.3.11. The aggregate impacts of both natural and human-induced physical damages to various coral life history stages, including adult mortality and fragmentation, settlement, polyp development, and juvenile growth. The overall contribution of physical damages to extinction risk for the 82 candidate coral species was determined to be low by the BRT. Diagram prepared by Amanda Toperoff, NOAA-PIFSC.

A large body of literature describes the effects of waves generated by tropical and extratropical cyclones on coral reefs, and several excellent reviews highlight tsunami effects (Stoddart, 1997; Wilkinson et al., 2006). Storms generally produce destructive waves for many hours or days at a time and often bring significant rainfall, while tsunamis add additional disturbance in the form of earthquakes and debris generated from coastal inundation. For the purposes of this

review, the BRT considers tsunami and cyclone effects to fundamentally be big-wave events and therefore somewhat comparable, although of different wave frequencies. Damage is typically patchy, depending on depth, wave exposure, and the existing biological community. Big-wave events generate coral fragments, and massive corals that are a century or older can be toppled (Bries et al., 2004). Storm waves and tsunamis can move massive amounts of sediment (Chavanich et al., 2005; Hubbard, 1992), abrading or burying corals in some parts of a reef (Woodley et al., 1981) while exposing previously buried substrates in others (Bries et al., 2004) and introducing anthropogenic and natural debris to coral reefs. Storm-induced fragmentation can enhance asexual reproduction in branching corals (Fong and Lirman, 1995; Lirman, 2000) but reduce the topographic complexity of reefs (Edmunds, 2002). Tropical cyclones often produce significant rain events, with the potential to produce hyposaline conditions that cause corals to bleach (Goreau, 1964; Van Woessik, 1991).

A well-documented example is Hurricane Allen in 1980 (Woodley et al., 1981), the first tropical cyclone to directly hit Jamaica in four decades. The storm produced substantial damage to some coral reef areas, but it was predicted to have little long-term effect on the reef because the return period of storms was longer than the time estimated for reef recovery (Graus et al., 1984). However, delayed mortality from predation, disease, or algal outbreaks exacerbated the storm effects and prolonged recovery (Knowlton et al., 1981). Macroalgal blooms following the 1983 mass mortality of *Diadema* further reduced coral cover (Hughes, 1994) and the subsequent passage of Hurricane Gilbert in 1988 delayed recovery still further (Oliver, 1992). A meta-analysis of monitoring data in the Caribbean found that coral cover at tropical cyclone-impacted sites was reduced by an average of 17% in the year following a storm, with no evidence of recovery for at least 8 years (Gardner et al., 2005). However, tropical cyclone damage is extremely patchy, depending on depth, wave exposure, the existing biological community, and previous disturbance history. For example, hurricane effects were highly variable at Buck Island National Park following the passage of Hurricane Hugo, as sites within a few hundred meters of each other showed substantial variability in coral mortality (Sammarco, 1980) and subsequent recovery (Bythell et al., 2000). Storm effects at landscape scales have been observed to be consistent with the intermediate disturbance hypothesis (Connell, 1978), although that may not hold for deeper reefs (Sussman et al., 2003). Coral cover and diversity in Belize were highest at sites of intermediate disturbance (Aronson and Precht, 1995), whereas landscape-scale coral community composition at Buck Island was stable over a decade despite hurricane impacts (Bythell et al., 2000).

Cyclone distribution is nonrandom in space and time. The return time of hurricanes in Central America was twice as long as that in Florida from 1980 to 2001 (Gardner et al., 2005). In the Lesser Antilles, hurricanes primarily strike Guadeloupe and Dominica, but rarely hit Trinidad, Tobago, and Grenada (Treml et al., 1997). Hindcast models of wave energy from historical cyclone tracks along the Great Barrier Reef predict that the northern portions of the Reef have lower risk of damage than elsewhere in the system (Puotinen, 2007). However, changing climate could induce changes in storm tracks, exposing normally-sheltered reefs to significant wave events. Deep reefs may provide some refuge from tropical cyclone effects (Lugo-Fernández and Gravois, 2010)—as may reefs within about 5 degrees of the equator, since cyclones rarely form or move within those latitudes, where the Coriolis force is weakest (Gray, 1998). Remote locations may benefit from storms via increased larval dispersal (Lugo-Fernández and Gravois, 2010).

Storms may or may not be increasing in frequency—over the last half of the 20th century, cyclone frequency has decreased in the Atlantic (Landsea et al., 1996) but increased in the western North Pacific (Chan and Shi, 1996). However, tropical storms do appear to be increasing in intensity (Emanuel, 2005; Webster et al., 2005), potentially increasing the severity of storm impacts to coral reefs. Recurrent storms become multiple stressors, and even a single storm event can be a multiple stressor with both short- and long-term effects (Hughes and Connell, 1999). The ability of corals to recover from acute events is reduced by chronic stresses (Connell et al., 1997). Increased bioerosion on eutrophic reefs and predicted reductions in skeletal density with ocean acidification could make reefs more vulnerable to physical storm damage (Hallock, 1988; Hallock and Schlager, 1986). A combination of stronger storms and slower recovery times would be expected to increase the effects of cyclones, even in the absence of more frequent storms. However, management actions could enhance resilience to storms—for example, reefs with conserved herbivory may be better able to maintain coral populations despite frequent tropical cyclone disturbances (Edwards et al., 2010).

3.3.8 Human-induced physical damage

Humans are quite effective at modifying nearshore coastal environments. In tropical areas, this often includes inflicting physical damage on coral reefs through both intentional use and accidents. These impacts have been reviewed across a variety of spatial scales (Chabanet et al., 2005). Reefs are affected by a diverse array of coastal construction activities, including land reclamation, airport and harbor construction, and mining for building materials (see (Maragos, 1993) for a regional review). Mining for building material removes both live coral and reef framework, which reduces coral cover and reduces fish habitat (Dulvy et al., 1995). Mining changes the topographic structure and creates low-resistance channels in the reef that increase coastal erosion and make the coast more vulnerable to extreme wave events such as tsunamis (Dulvy et al., 1995; Fernando et al., 2005). Construction activities can have indirect effects as well—for example, dredging is often associated with turbidity effects that harm corals or slow coral growth (Dodge and Vaisnys, 1977; Eakin et al., 1994), while drilling rigs can create a halo of coral loss around the rig (Hudson et al., 1982).

Coastal construction and development are intentional actions, offering the potential to “rescue” corals in the affected zone prior to the impact; however, this is a costly endeavor. Vessel groundings and other accidental injuries do not offer the same possibilities. Large-vessel groundings physically destroy or injure corals in ways similar to cyclones, but also turn the reef framework into rubble (Hudson and Diaz, 1988). Vessel anchors can also cause similar types of damage to corals (Rogers and Garrison, 2001); the effects are often smaller in scale but more frequently inflicted. Grounded vessels can release harmful chemicals into the reef environment (Hawkins et al., 1991) and leave behind antifouling paint that inhibits the ability of corals to recruit into the injury (Jones, 2007; Negri et al., 2002). Injuries from groundings and anchor deployments can take decades or centuries to recover (Riegl, 2001; Rogers and Garrison, 2001), or induce phase-shifts to non-coral communities (Hatcher, 1984; Work et al., 2008). Managers can reduce the potential for groundings or anchor injuries through establishing protected areas or installing aids to navigation. For example, the Florida Keys National Marine Sanctuary (FKNMS) was established in 1990, and a major impetus for the legislation was the three large-vessel groundings that occurred in an 18-day period in 1989. The FKNMS has observed a decrease in large-vessel groundings since its inception, but smaller impacts from recreational and fishing vessels are still a persistent problem. Over the last decade, there have been on average ~ 500 reported vessel groundings per year within the FKNMS. Of these, about 85% have been in seagrass-dominated habitats while the remainder have impacted shallow coral reef and hard bottom habitats (FKNMS, unpubl. data).

Recreational and fishing activities can result in “accidental” physical injuries as well. The physical effects of dynamite “blast fishing” are similar to those of groundings (Riegl, 2001); the harmful effects of fishing are evaluated in more detail in Section 3.3.4. Marine debris such as derelict fishing gear, from large commercial nets to fish traps to recreational fishing line, can cause coral damage; these effects are considered more explicitly in Section 3.3.5. Tourists and recreational users can cause substantial physical injury from trampling and scuba diving. Branching corals are most vulnerable to these sorts of unintentional breakage (Hawkins and Roberts, 1992). Where trampling does not induce mortality, it can still reduce coral growth (Rodgers et al., 2003) and/or resuspend sediment that can stress corals (Neil, 1990). Tourist and recreational damage can lead to a reduction in overall colony size (Hawkins and Roberts, 1993) or alter community structure (Kay and Liddle, 1989). Vulnerability to damage may vary by reef zone (Hawkins and Roberts, 1993); for example, little damage would be expected if fragile corals are located deeper than snorkeling depth (Meyer and Holland, 2008). Some reefs may be able to withstand high usage levels (Hawkins and Roberts, 1992) while in others damage depends on the level of human use (Rodgers and Cox, 2003). Increasing tourism and recreational use can potentially be managed by evaluating “carrying capacity” for reef sites and limiting access accordingly (Hawkins and Roberts, 1997).

The recent Reefs at Risk Revisited report (Burke et al., 2011) provided a global analysis of risk to coral reefs, by region and globally, to the impacts of coastal development (Fig. 3.3.12). While the coastal development threats categorized in their analysis do not map perfectly with the human-induced physical damage threats discussed in this section, it is instructive to note the similarities of their independently derived conclusions.

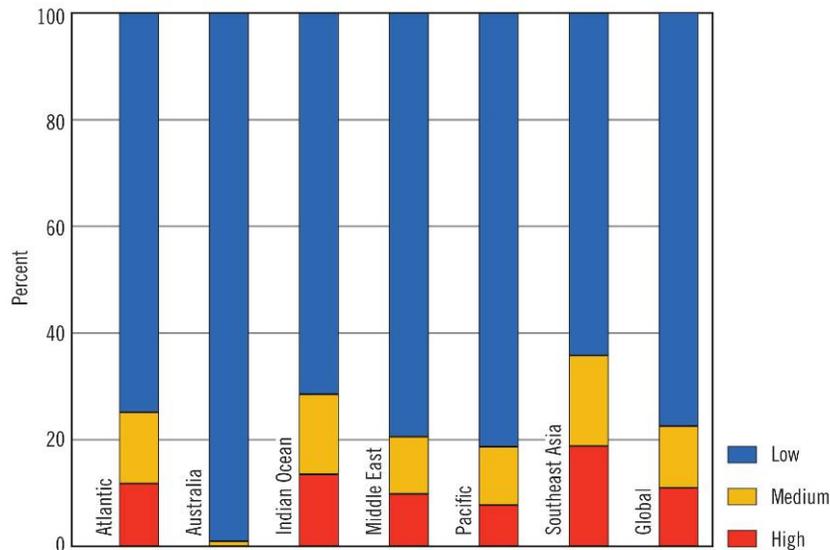


Figure 3.3.12. Global analysis of risk to coral reefs, by region and globally, to the impacts of coastal development. Risk was assessed through a GIS-based analysis of risk compiled from all available sources and categorized as low, medium or high threat to reefs in the region. For details on methods and a full description of threats included in this risk category, please see the original publication. From Reefs at Risk Revisited (Burke et al., 2011).

3.3.9 Aquatic invasive species

Although the introduction of nonindigenous species is seen as one of the largest threats to global biodiversity (Vitousek et al., 1997), less is known about invasion ecology of coral reefs. In other marine environments, alien species have been shown to have major negative effects on the receiving communities where they often outcompete native species, reduce species diversity, change community structure, reduce productivity and disrupt food web functioning by altering energy flow among trophic levels (Carlton, 1996; 2002; Grosholz, 2002; Ruiz et al., 2000; Ruiz et al., 1999; Stachowicz and Byrnes, 2006; Williams, 2007). The lack of information regarding effects of species introductions on coral reefs suggests that invasive species have not been well studied or that there have been few successful invasions in these systems (Coles and Eldredge, 2002). There is a need to understand the role of invasive species in the decline of coral reef ecosystem health in order to effectively manage and restore these systems in the face of global change and the full suite of stressors.

3.3.9.1 Introduced marine invertebrates

Introduced marine invertebrate species, along with their associated diseases and symbionts, are spreading throughout the tropical seas. This is substantially increasing the number of marine invertebrate species in some harbors, especially in the more isolated archipelagoes, and this 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 the introduced species is most often in protected ports or harbors, and so introduced marine invertebrates tend to be from backwaters. 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 to date been ecologically inconsequential on the open coast coral reefs (Paulay et al., 2002). Guam has 276 reef-building coral species (Paulay et al., 2002); within Apra Harbor, there are well-developed reefs with a rich coral fauna and some of the highest coral cover on Guam. Even within the harbor, the 79 introduced species generally tend to occupy artificial substrata (Paulay et al., 2002). Hawai'i has only about a quarter of the number of coral species as Guam and some invasive invertebrates have been found in some of the sheltered reef waters. The bright red sponge *Mycale armata* has become predominant on coral reefs in parts of Kāne`ohe Bay and the small introduced barnacle *Chthamalus proteus* has compressed the niches of three other alien barnacle species. In Hawai'i, 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). It has been suggested that reefs with a diverse indigenous assemblage

are difficult to invade. There has been no evidence to date of invasive species influencing coral reproduction or larval stages, so their effects are limited to life stages from settlement to adulthood (Fig. 3.3.13).

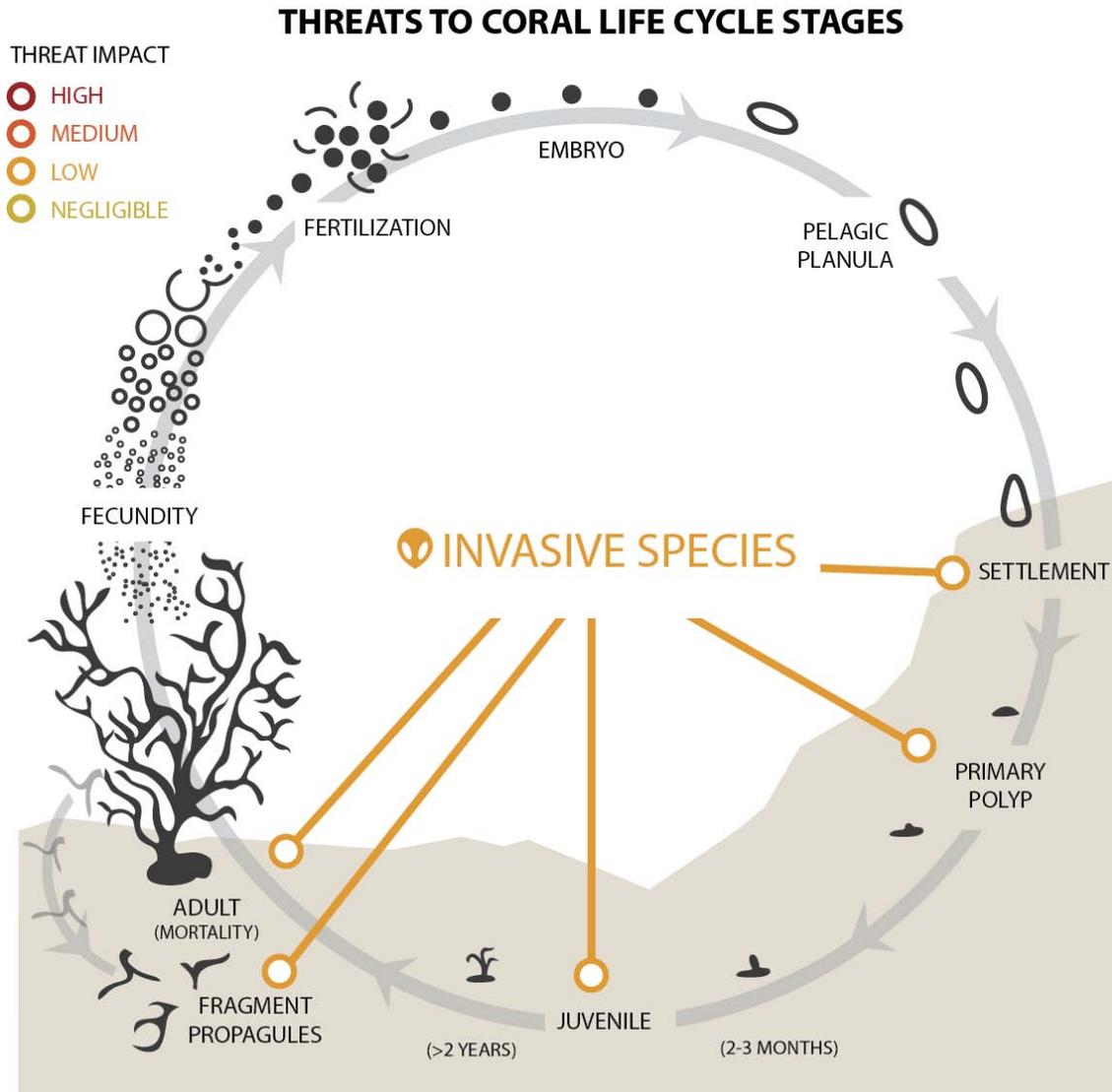


Figure 3.3.13. The impacts of invasive species to various coral life history stages, including adult mortality and fragmentation, settlement, polyp development, and juvenile growth. The overall contribution of invasive species to extinction risk for the 82 candidate coral species was determined to be **low** by the BRT. Diagram prepared by Amanda Toperoff, NOAA-PIFSC.

3.3.9.2 Introduced corals

The only known case of a major invasion of an alien species of coral affecting community structure is that of *Carijoa riisei*, an octocoral. The breeding stock of *Carijoa riisei* probably arrived in Pearl Harbor, Hawai'i, attached to the hull of a ship. Marine biological surveys were conducted in the 1930s and 1940s that included studies of the fouling communities of Pearl Harbor, but *Carijoa riisei* was absent from these surveys (Kahng, 2006). It was first recorded on O`ahu in 1966 (Kahng, 2006) and in Pearl Harbor in 1972 (Kahng and Grigg, 2005). Surveys of the black coral industry up to 1998 did not report *Carijoa riisei* (Kahng, 2006), but by 2001 it was found in deep offshore waters overgrowing antipatharians (black corals) in Au`au Channel (between Lana`i and Maui) on a large scale (Kahng and Grigg, 2005). The ultimate outcome of this invasion of an introduced octocoral is an increase in the number of species. *Carijoa riisei* uses the commercially valuable black corals *Antipathes dichotoma* and *Antipathes grandis* as substrata, smothering them and seriously affecting the \$30 million precious coral industry in Hawai'i. *Carijoa riisei* has a major effect on black coral populations between the depths of 70 and 105 m. *Carijoa riisei* is sensitive to direct sunlight above 70 m and especially above 40 m where it is only found on underhangs and other shaded locations. Below 105-m depth in the

Au`au Channel is a thermocline, a drop from 26°C to 22°C, and below this *Carijoa riisei* is less prevalent and aggressive. The final outcome is that the number of species increased by one octocoral along with associates, and the two black corals experienced reduction in abundance between the depths of 70 m and 105 m.

Other cases of introduced corals have also indicated increased species numbers, but these other cases have not induced major changes in community structure. A very small population of *Siderastrea siderea* has established itself from the Caribbean to just beyond the Pacific entrance of the Panama Canal. Originally thought to be a new species, *Siderastrea glynni* (Budd and Guzman, 1994), it does not appear to have spread and has been found only in the Gulf of Panama (Maté, 2003a), but it has since been determined to be genetically identical to *Siderastrea siderea* (Forsman et al., 2005). The azooxanthellate scleractinian *Tubastrea coccinea* became established in the western Atlantic in the 1940s and is now very abundant and widespread, especially on artificial substrata (Fenner and Banks, 2004). *Tubastrea micrantha* has just become established on one oil rig near Louisiana. *Tubastraea micrantha* will probably also spread, but it is possible that both *Tubastrea* species will tend to occupy artificial substrata and not invade coral reefs to a major extent. Both *Tubastraea coccinea* and *Tubastraea tagusensis* invaded the geographic region south of the Amazon in the 1980s and have recently extended their ranges 130 km farther to the southwest in Brazil (Mantelatto et al., 2011). *Tubastraea coccinea* and *Tubastraea tagusensis* are usually found on vertical substrata and underhangs, but can appear to dominate rocky substrata on which reef-building scleractinians *Madracis decactis* and the endemic *Mussimilia hispida* are found (Mantelatto et al. 2011).

3.3.9.3 *Introduced algae*

In some cases, alien species introductions are not accidental. Some of the algal species that have become invasive in Hawai`i were introduced deliberately for aquaculture because of their characteristics of rapid growth and productivity. These characteristics, desirable for culturing, clearly increase the potential invasiveness of such species by making them potential competitive dominants. The red carrageenan-producing algae *Eucheuma denticulatum* and *Kappaphycus* spp. were intentionally introduced to Kāne`ohe Bay and Honolulu Harbor in the 1970s for experimental aquaculture (Eldredge, 1994) and introduced to many other areas around the tropics (Castelar et al., 2009). *Eucheuma* in particular has become highly invasive in Hawai`i where it overgrows and kills reef-building corals and reduces species diversity and habitat complexity. Recent reports suggest that this species has also become invasive on other tropical reefs in the central Pacific where it has also been intentionally introduced. *Kappaphycus alvarezii* introduced into southern India for mariculture has been documented overgrowing and killing *Acropora* spp. corals (Chandrasekaran et al., 2008).

Alien algal impacts on corals are best documented in Hawai`i and different species show different patterns of spread. Three invasive red algal species *Gracilaria salicornia*, *Hypnea musciformis*, and *Eucheuma denticulatum* are known to form extensive, destructive blooms and have been observed overgrowing reef-building corals in Kāne`ohe Bay, the south shore of O`ahu Island including the Waikiki area, and the south shore of Moloka`i Island, which harbors some of Hawai`i's most intact and expansive coral reef ecosystems (Eldredge and Smith, 2001; Rodgers and Cox, 1999; Russell, 1992; Russell and Balazs, 1994; Smith et al., 2004a; Smith et al., 2002). The red alga *Gracilaria salicornia* was most likely an accidental introduction via the shipping industry in the 1950s. Later in the 1970s this species was transported to O`ahu and Moloka`i (Eldredge, 1994) for experimental aquaculture and while it is still restricted to these three islands it has spread extensively within each island, most notably O`ahu where it is the single most dominant species in Waikiki and parts of Kāne`ohe Bay and evidence suggests that it is continuing to spread (Smith et al., 2004a). *Hypnea musciformis* was initially introduced to O`ahu and can now be found around all of the main Hawaiian Islands aside from Hawai`i (as of 2003) but is most abundant around the Maui Island where it forms large, often mono-specific blooms. This species seems to be restricted to shallow reef flat and back reef habitats and appears to be associated with reduced water quality (Smith et al., 2006).

The most widespread of the various invasive algae is the red alga *Acanthophora spicifera* which was initially introduced to O`ahu Island via hull fouling. This species has now been found across all of the main Hawaiian Islands and seems to be restricted mostly to shallow water habitats, although recent deeper water populations have been identified around Maui Island. This species is one of the most preferred food resources for herbivorous fishes in Hawai`i and so it is likely to be less abundant where herbivores are common (Conklin, 2007).

Most healthy coral reef ecosystems are dominated by reef-building corals and crustose coralline algae since most of the turf and macroalgal production is consumed by grazers (fish and urchins); diverse algal assemblages are restricted to areas that are relatively inaccessible to herbivores (Carpenter, 1986; Carpenter, 1983). However, numerous natural and anthropogenic impacts can allow algae to proliferate and gain a competitive advantage over the slower growing corals

(Hughes et al., 1999a; Lapointe, 1999). Fishing of herbivorous fishes and/or the addition of inorganic nitrogen and phosphorus can both act to increase the abundance of algae on reefs but individual algal species are likely to respond differently to changes in nutrient levels and grazing pressure (Miller et al., 1999; Smith et al., 2001; Thacker et al., 2001). Herbivores will have the strongest top-down control on species of algae that are preferred food sources; nutrient enrichment will have the greatest bottom-up control on algae that are able to rapidly take up and assimilate nutrients. Additionally, numerous physical variables affect the abundance and distribution of different species of algae such as light, temperature, salinity, flow and substratum type.

3.3.9.4 Introduced fish: lionfish in the Caribbean

Two species of lionfish have become an emergent exotic invasive marine fish, species that have taken hold in the South Atlantic and Caribbean during the past decade with massive increases in distribution and density (http://fl.biology.usgs.gov/lionfish_progression/lionfish_progression.html). The Indo-Pacific lionfishes, *Pterois volitans* and *Pterois miles*, were first documented in South Florida waters as early as 1992 with the unintentional release of at least six lionfish from a home aquarium into Biscayne Bay during Hurricane Andrew (Courtenay, 1995). It is likely that additional isolated releases by aquarium owners have also occurred following the documented 1992 release, since lionfishes are among the most sought-after aquarium species (Balboa, 2003) and can become unwanted aquarium inhabitants that consume other aquarium life. Widely-distributed early sightings suggest multiple introductions and the source of the current, successful expansion of lionfish is unclear. Since then, lionfish have rapidly and successfully spread throughout western Atlantic waters, from the southern Caribbean to as far north as Rhode Island (although winter sea temperatures appear to restrict over-wintering success to areas south of Cape Hatteras, North Carolina). Currently, two of the largest known lionfish populations occur in North Carolina (Whitfield et al., 2007) and the Bahamas (Government of the Bahamas 2005), although lionfish are now being reported from all nations and reef areas of the Caribbean and Gulf of Mexico except for the southern Lesser Antilles USGS (USGS, 2010).

As of 2009 (Schofield, 2009), lionfish had become established along the U.S. Atlantic coast from Cape Hatteras, North Carolina to Miami, Florida (since 2002), in Bermuda (2004), Bahamas (2005), Turks and Caicos (2008) and the Cayman Islands (2009), the Greater Antilles: Cuba (2007), Jamaica (2008), Hispaniola (2008) and Puerto Rico (2009), the northern Lesser Antilles only from St. Croix (2008), and Central and South America: Mexico, Honduras and Costa Rica (2009). Since that time, lionfish have been sighted in the Gulf of Mexico: northern Yucatan peninsula (December 2009), Dry Tortugas National Park (June 2010), Key West (July 2010), the west coast of peninsular Florida (Manatee and Pinellas counties; beginning August 2010), Pensacola (Florida) as well as the Alabama and Louisiana coasts; the Lesser Antilles: St. Croix, St. Thomas and St. John (including Virgin Islands National Park), Barbuda, Saba and Sint Maarten in July 2010, Aruba, Bonaire and Curacao (Netherlands Antilles) in 2009; and the Caribbean coast of Central and South America: Belize, Nicaragua, Panamá, Columbia and Venezuela.

Lionfish are ambush predators; studies suggest that there is very little that these fish will not eat (Raloff, 2006). These fish appear to be feeding primarily on the same food items as the commercially and ecologically important snapper-grouper complex within the coral reef environment, as well as juvenile parrotfish (Raloff, 2006) and strongly impair recruitment of native fishes (Albins and Hixon, 2008). Trophic impacts of lionfish may be relatively greater than those of native predators since they are not recognized by native prey that hence fail to display appropriate avoidance behaviors (Anton et al., 2010).

The impacts of lionfish on reef food webs or on corals are unknown at this early stage of their invasion, but in the absence of natural predators, these invasive species have a potential to precipitate significant changes in the coral reef fish complex, with unknown cascading impacts to the corals. Lionfish are potentially exacerbating trophic cascade effects, especially through the loss of herbivores and their control of algal growth.

3.3.10 Summary of local changes and their impacts

The activities of human societies in local areas, as well as natural phenomena, have contributed to observed coral population declines in many if not all human-inhabited regions of the world. Although they are natural phenomena, storms, predation, and to some extent disease are recognized as having potential depensatory effects as coral populations decline. In many locations, the impacts of these threats are acute and severe, and many of the individual local threats described in the previous sections are present across such wide geographic areas and at such intensities that their impacts are in some sense not “local” at all, but rather regional or even global.

A very recent independent global analysis of threats to coral reefs, Reefs at Risk Revisited (Burke et al., 2011), was released subsequent to the BRT’s original evaluation. Their analyses ranked risks from different threats on a geographic basis, based on characteristics such as human population, development (size of adjacent cities, ports, hotels, etc), and agricultural and watershed status (deforestation, river drainage, etc.). While the threats categorized in their analysis do not map perfectly to those used in this Status Review Report, it is instructive to consider the three local threat rankings and drivers in their analyses (Table 3.3.2) as one way to extrapolate the sometimes-dramatic impacts of local anthropogenic stressors to a global threat ranking. Figure 3.3.14 also shows how Reefs at Risk Revisited (Burke et al., 2011) ranked their index of integrated local threats for various regions around the world.

Table 3.3.2. Summary of local reef threats as described by Reefs at Risk Revisited (Burke et al., 2011).

RRR local threat	Components and drivers (Burke et al. 2011)	% of reefs ranked Med or High risk	Future trend	Corresponding Status Review Threat
Fishing* and Destructive Fishing Practices	Human population growth, lack of alternative livelihoods, poor management	>55%	Increase	Fishing: Trophic Cascade, Fishing: Habitat Impacts
Coastal Development	Construction, Sewage, Tourism (Hotels, Airports), sea ports, size of nearby cities	< 25%	Increase	Human Physical Disturbance, Land Based Sources of Pollution
Watershed-based pollution	Deforestation, erosion, sedimentation, agricultural pollution	<30%	Increase	Land Based Sources of Pollution
* Burke et al. use the term “overfishing”. We instead use the more general term fishing as the capture and removal of fish from the ecosystem.				

Based on increases in human populations, Reefs at Risk Revisited (Burke et al. 2011) estimated that the overfishing threat has increased the most (of the local threats) over the past decade. The disproportionately faster growth of human population in coastal regions means that these anthropogenic local threats are expected to continue growing into the future.

The Reefs at Risk Revisited (Burke et al. 2011) report was published when the BRT was nearing completion of this report. After reviewing that document, the BRT chose not to change risk evaluations for any of the 82 candidate coral species based on the Reefs at Risk Revisited (Burke et al. 2011) analyses. However, the BRT decided to provide some of the information on the regional to global assessments of Burke et al. as they relate to the threats discussed by the BRT. Overall, the ranking of the local anthropogenic threats by Reefs at Risk Revisited (Burke et al. 2011) was consistent with the BRT’s conclusions that local anthropogenic threats (fishing, LBSP, physical damage) are of medium to low importance in posing extinction risk to the 82 candidate coral species. The Reefs at Risk Revisited (Burke et al. 2011) analyses did not assess coral disease (assessed as a **high** extinction threat in this Status Review Report) as a separate threat because of uncertainty and complexity in its drivers.

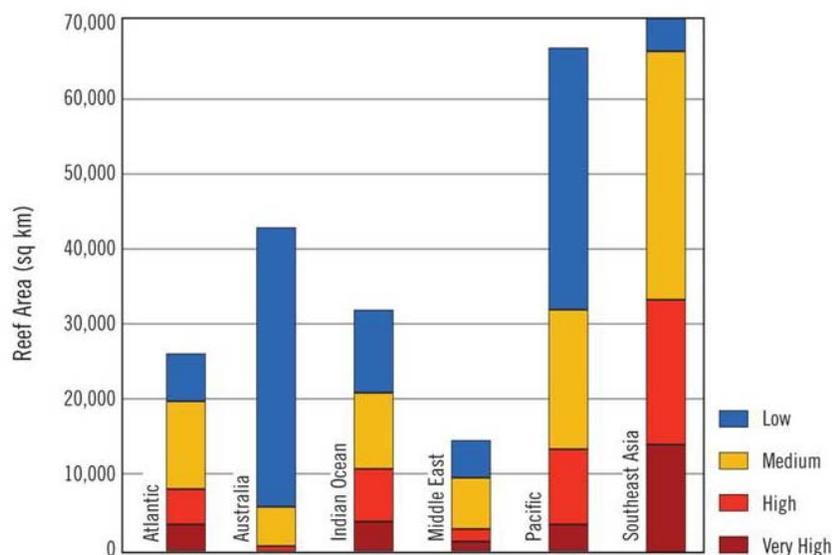


Figure 3.3.14. Global analysis of risk to coral reefs, by region, to an integrated local threat index. Risk was assessed through a GIS-based analysis of risk compiled from all available sources and categorized as low, medium or high threat to reefs. For details on methods and a full description of threats included, please see the original publication. Used with permission from Reefs at Risk Revisited (Burke et al., 2011).

3.4 Interactive and Unapparent Threats on Coral Populations

Scientific knowledge of most of the individual threats discussed in this chapter is not nearly as precise or as extensive as preferred. More concerning, the synergistic and cumulative effects of these threats are even less well understood. Some documentation of patterns and experimental research indicate that the cumulative or interactive effects of multiple individual threats can be greater than their sum, but certain threats can also ameliorate each other (Darling and Côté, 2008). It is also clear that some of these threats are novel (e.g., contaminants outside the species' evolutionary experience), occur in new and severe combinations or change at unprecedented rates (e.g., atmospheric CO₂). Although the term “synergy” may be ambiguously applied in the coral literature (Dunne, 2010), it is clear that multiple stressors affect corals simultaneously, whether the effects are cumulative (the sum of individual stresses) or interactive (e.g., synergistic or antagonistic).

One example of such interactive threats involves the growing evidence that degraded water quality can lower the thermal bleaching threshold for corals. That is, bleaching is more likely to occur at lower temperatures when corals are experiencing physiological stress from poor water quality. Evidence for this comes from both spatial and temporal comparisons in both the Caribbean and Indo-Pacific basins (Carilli et al., 2009a; Carilli et al., 2009b; Wooldridge, 2009b; Wooldridge and Done, 2009) and at least one mechanism to incorporate the combination of these stressors has been proposed (Wooldridge, 2009a). Another interactive effect involving bleaching is a similar increase in sensitivity to high temperatures as a result of ocean acidification (Anthony et al., 2008), perhaps through increased photo-acclimation (Crawley et al., 2010). Another example involves the linked effects of fishing, coral predation, and disease. It is likely that in some cases, the removal of apex predators by fishing leads to release of some coral predators such as butterflyfish (Raymundo et al., 2009). Butterflyfishes affect corals both directly by preying on polyps, but also indirectly by vectoring disease conditions (Aeby and Santavy, 2006). Hence, the influence of disease on a given coral population may be exacerbated when fishing causes an increase in butterflyfish populations, or potentially other disease-vectoring corallivores. Not all interactive effects are negative; for example, although corals are commonly stressed by sediment, there is some suggestion that turbidity and colored dissolved organic materials in the water column may provide some shelter from bleaching, presumably by reducing ultraviolet radiation (Goreau et al., 2000). However, this is neither a reliable, nor well-tested attribute of bleaching resistance (West and Salm, 2003).

Unapparent effects are another complexity in assessing the individual and overall extinction risks to coral species. A great portion of coral life history is difficult or nearly impossible to observe directly (spawning, fertilization, planktonic planulae, settlement, and early years of the post-settlement period). Our limited understanding of these threats comes from supposition and limited laboratory experiments (Negri et al., 2007; Vermeij et al., 2006) with virtually no opportunity to validate laboratory-based results in natural coral reef systems. For example, post-settlement growth or mortality rates can, with difficulty, be measured in the lab with and without experimental stressors, but very few examples with comparable field data exist. Hughes et al. (2000) measured the relationship between spatio-temporal variation in fecundity and recruitment by acroporids. They found that declines in coral fecundity and spawning have a disproportionate effect on recruitment. Similarly, while field manipulations have shown that elevated nutrients can reduce coral fecundity, there are no known approaches to quantify what the effect of that reduced fecundity would mean for coral recruitment. The specific threats and their relative importance in these cryptic life history phases are essentially invisible in terms of population assessment and, hence, impossible to apply with confidence in assessing extinction risk.

Additional examples of these effects are discussed in the threat accounts elsewhere in this chapter. It is logical to conclude that these interactive and often unapparent effects of stressors will combine to pose larger and less predictable threats than the sum of any individual stressors independently. The BRT acknowledges that unpredictable and sudden shifts in the population status for specific coral species have occurred and continue to be likely. However, the expectation is that the vast majority of such “surprises” will have negative consequences for coral populations. A notable exception is the interaction of fishing and bleaching on Kenyan coral reefs—fishing reduced coral cover by 51% and bleaching by 74%, but the two effects were either antagonistic or weakly additive in combination (Darling et al., 2010).

3.5 Summary of Threats

A range of threats, both natural and anthropogenic, and some that fall somewhat in between are described in varying levels of detail throughout this chapter, depending on both the level of risk they are projected to pose to coral extinction and the amount of relevant information available. While local threats such as fishing and land-based pollution are recognized as responsible for much of the coral decline that has been observed in the past, the best scientific information suggests that widespread coral disease effects and thermally-induced coral bleaching that have already devastated coral populations are manifestations of global climate change. The BRT considers ocean warming, ocean acidification, and disease to be overarching and influential in posing extinction risk to each of the 82 candidate coral species. These impacts are or are expected to become ubiquitous, and pose direct population disturbances (mortality and/or impaired recruitment) in varying degrees to each of the candidate coral species. There is also a category of threats (some of which have been responsible for great coral declines in the past) that the BRT considers important to coral reef ecosystems but of medium influence in posing extinction risk because their effects on coral populations are largely indirect and/or local to regional in spatial scale. This category includes fishing, sea level rise, and water quality issues related to sedimentation and eutrophication. Threats can be locally acute, but because they affect limited geographic areas, are considered to be of minor overall importance in posing extinction risk. Examples in this category are physical damage from storms or ship groundings, predator outbreaks, or collection for the ornamental trade. These types of threats, although minor overall, can be important in special cases, such as for species that have extremely narrow geographic ranges and/or at severely depleted population levels. Table 3.5.1 summarizes the proximate threats ordered by estimated importance for extinction risk. The discussion of threats in this chapter was organized by logical theme, not estimated importance. The recent *Reefs at Risk Revisited* (Burke et al., 2011) report summarized their assessment of reef threats and is provided below (Fig. 3.5.1).

It is critical to note that although the BRT has necessarily separated stresses for clarity of presentation, in nature it is much more common for multiple stressors to affect reefs simultaneously (Hughes et al., 2003; Hughes and Connell, 1999). Untangling the effects of interactive stressors is not trivial (Dunne, 2010), and stressors may interact in linear or nonlinear and positive or negative ways (Carilli et al., 2010; Darling et al., 2010; Porter et al., 1999). Further, stressor effects are often species-specific. Consequently, it may be difficult to attribute specific causes for observed biological changes in the absence of long-term observations, or to scale up interactive effects from the laboratory to field scenarios.

Table 3.5.1. Summary of proximate threats considered by the BRT in assessing extinction risks to the 82 candidate coral species. The ultimate factor for each of these proximate threats, excepting natural physical damage and changes in insolation, is growth in human population and consumption of natural resources. The table is ordered by the BRT estimate of the threat’s importance for extinction risk. Insolation was noted by the BRT to be particularly uncertain in the predictions of whether and with what intensity it would occur (while corals response to light is reasonably well understood).

Section	Scale	Proximate Threat	Importance
3.2.1	Global	Ocean Warming	High
3.3.2	Local	Disease	High
3.2.2	Global	Ocean Acidification	Med-High
3.3.4	Local	Reef Fishing—Trophic Effects	Medium
3.3.1	Local	Sedimentation	Low-Medium
3.3.1	Local	Nutrients	Low-Medium
3.2.3	Global	Sea-Level Rise	Low-Medium
3.3.1	Local	Toxins	Low
3.2.4	Global	Changing Ocean Circulation	Low
3.2.5	Global	Changing Storm Tracks/Intensities	Low
3.3.3	Local	Predation	Low
3.3.5	Local	Reef Fishing—Habitat Impacts /Destructive Fishing Practices	Low
3.3.6	Local	Ornamental Trade	Low
3.3.7	Local	Natural Physical Damage	Low
3.3.8	Local	Human-induced Physical Damage	Negligible-Low
3.3.9	Local	Aquatic Invasive Species	Negligible-Low
3.3.1	Local	Salinity	Negligible
3.2.6	Local	African/Asian Dust	Negligible
3.2.7	Global	Changes in Insolation	Probably Negligible

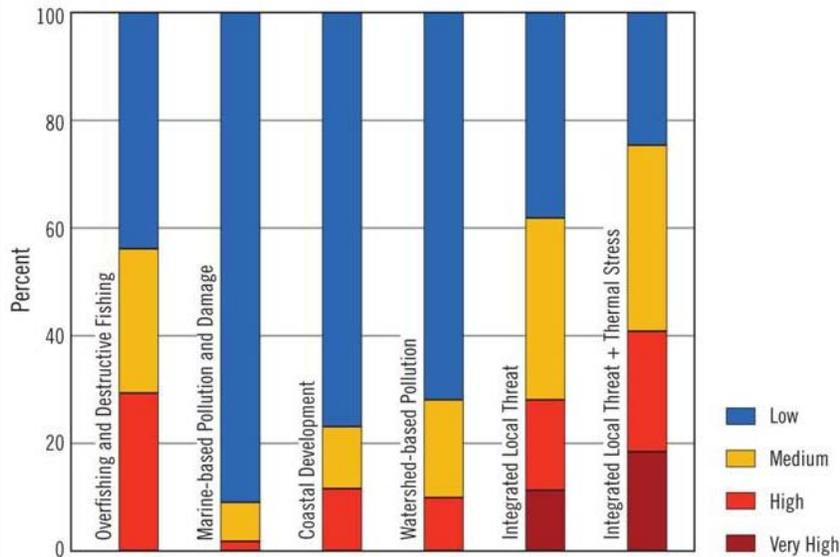


Figure 3.5.1. Global analysis of risk to coral reefs, by region and globally, to the four categories of local threat plus an integrated local threat and local threat plus thermal stress. Risk was assessed through a GIS-based analysis of risk compiled from all available sources and categorized as low, medium or high threat to reefs. For details on methods and a full description of threats included in each risk category, please see the original publication. Used with permission from Reefs at Risk Revisited (Burke et al., 2011).