We are IntechOpen,
the world's leading publisher of
Open Access books
Built by scientists, for scientists

4,800
Open access books available

122,000
International authors and editors

135M
Downloads

154
Countries delivered to

Our authors are among the

TOP 1%
most cited scientists

12.2%
Contributors from top 500 universities

BOOK CITATION INDEX
CLARIVATE ANALYTICS
INDEXED

WEB OF SCIENCE™

Selection of our books indexed in the Book Citation Index
in Web of Science™ Core Collection (BKCI)

Interested in publishing with us?
Contact book.department@intechopen.com

Numbers displayed above are based on latest data collected.
For more information visit www.intechopen.com

Coral Reef Bleaching: An Ecological and Biological Overview

Norma Olguín-López, Carolina Gutiérrez-Chávez,

Víctor Hugo Hérnández-Elizárraga,

César Ibarra-Alvarado and Alejandra Rojas-Molina

Abstract

Coral reefs are central to the biology of our planet, but in the past few decades, they have suffered a severe decline due to a variety of natural and anthropogenic disturbances. On a worldwide scale, the main disturbance is bleaching, which can be defined as the loss of endosymbiotic dinoflagellates and/or of their photosynthetic pigments from their cnidarian host; with that, the normal pigmentation of the tissue of cnidarians is generally lost and the white calcium carbonate skeleton becomes visible through the transparent tissue of the host. Coral bleaching can be triggered by multiple factors, but most of the bleaching observed in the field is a result of elevated sea surface temperature. It has been widely documented that bleaching is deleterious to coral reefs, significantly altering the biological and ecological processes that maintain reef communities; yet populations resistant to climate change have recently been identified, and it has been reported that acclimatization occurs in less than two years. The aim of this review is to provide up-to-date information regarding cnidarian-dinoflagellate symbiosis; causes of coral bleaching; mechanisms underlying this phenomenon; consequences of bleaching; and the survival mechanisms by which coral reefs face this threat.

Keywords: cnidarians, coral bleaching, global warming, marine ecosystem, symbiotic dinoflagellates, *Symbiodinium*

1. Introduction

Despite occupying only 0.1% of the ocean, coral reefs play a critical role in marine ecology, and in human sustainability, they are invaluable from a variety of perspectives. They are home to more than a quarter of all the species that inhabit the ocean, provide coastal protection, and support more than 10 millions of people living on tropical coasts [1, 2]. Economic goods and ecosystem services of coral reefs are worth more than US $20 trillion annually [3].

Coral reefs are central to the biology of our planet; in terms of biodiversity, they are the most rich, complex, and productive marine ecosystem on Earth. It has been estimated that over 90% of the species inhabiting coral reefs have yet to be described [4]. Therefore, it is not surprising that the organisms that constitute these ecosystems produce a great variety of molecules with unique structural characteristics that exhibit numerous biological activities [5], and are considered a rich source of novel bioactive agents with great pharmaceutical and biotechnological potential [6].

Unfortunately, coral reefs are extremely susceptible to the stress related to greenhouse gas emissions, particularly ocean warming and acidification [7–10], which provoke disturbances that can seriously affect and break down the homeostatic capacity of coral reefs to overcome stressors [11]. One of these disturbances is the event called "bleaching," in which the tissues of corals and hydrocorals lose their photosynthetic endosymbiotic zooxanthellae (dinoflagellate algae of the genus *Symbiodinium*) or their pigments, which exposes the white exoskeleton of calcium carbonate [12–14].

Numerous studies have shown that bleaching is harmful to coral reefs, since it significantly alters the biological and ecological processes that maintain equilibrium in the reef communities. Bleaching episodes have resulted in massive damage to coral reefs around the world, with serious effects on the maintenance of biodiversity in the marine tropics. Bleaching is also responsible for other declines in reef health, such as the increase in coral diseases, declines in reef calcification, the breakdown of reef framework by bioeroders, and the loss of critical habitat for associated reef organisms [15–18]. Climate models predict that, if CO_2 emissions continue to rise at the current rate, bleaching events will increase in frequency and severity, threatening the survival of coral reefs. Actually, it has been projected that 90% of coral reefs around the world will be at risk if bleaching events occur annually [15, 16, 19].

The US National Oceanic and Atmospheric Administration (NOAA) coral reef watch, the Global Coral Reef Monitoring Network (GCRMN), as well as other environmental agencies around the world have been monitoring mass coral bleaching events for more than a decade, in order to understand conditions that cause bleaching and to develop measures to rehabilitate reefs [1–20]. On the other hand, academic researchers have addressed the study of this phenomenon employing different approaches, including genomics, transcriptomics, and proteomics to better comprehend the molecular mechanisms that provoke it, its consequences, and the potential adaptive response of cnidarians to this condition [21–29]. Undoubtedly, bleaching represents an enormous threat to the survival of coral reefs, as bleached organisms display an increased susceptibility to pathogens, a decreased resistance to predators

and bioeroders, declines in reef calcification, depressed growth and reproduction rates, and a lessening of ability to repair damages [15–18]. In this context, the purpose of this review is to provide updated information regarding cnidarian-dinoflagellate symbiosis; causes and consequences of coral bleaching; the molecular processes underlying this phenomenon; and the survival mechanisms by which coral reefs face this threat.

1.1. Search strategy

The literature consulted corresponds to the main reviews and articles explaining the phenomenon of bleaching, which contributes to the understanding of the relationship between the causes, mechanisms, and consequences of bleaching.

2. Cnidarian-dinoflagellate symbiosis

An important feature of coral reef ecosystems is that most of the 798 reef-forming species have developed a mutualistic symbiosis with unicellular dinoflagellate algae of the genus *Symbiodinium*, commonly referred to as zooxanthellae (**Figure 1**). This symbiosis is essential in the formation of large and important structures in coral reefs [30]. The genus *Symbiodinium* encompasses nine major clades (A to I), most of which were identified based on the ribosomal DNA small subunit [31]. These tiny organisms (8–10 μm in diameter) live within cnidarian cells, inside a host-derived vacuole (symbiosome) located within the gastrodermal cell layer. Under normal conditions, the population density of symbionts ranges from 0.5 to 5×10^6 cells per cm^2 of coral surface, although the limits of this range may vary [30, 32]. Regulation of symbiont density involves different mechanisms, such as limiting the nutrients delivered from corals to symbionts, digesting photosynthetic algae, expulsing excess symbionts, rearranging excess symbionts into new coral cells, and producing growth inhibition factors [30, 33–35].

Symbiodinium algae carry out photosynthesis, but instead of retaining the sugars and amino acids that result from this activity for their own growth and reproduction, they deliver more than 95% of their photosynthetic production to their host. In return, *Symbiodinium* has direct access to the waste products of coral metabolism, such as carbon dioxide, which is used in photosynthesis. The recycling of nutrients between coral host and its endosymbionts is extremely efficient and allows them to live in nutrient-poor waters [30, 35, 36]. Endosymbionts translocate molecular oxygen to their hosts and most of their photosynthetically-fixed carbon in the form of glycerol, glucose, amino acids, and lipids. Moreover, the oxygen produced during photosynthesis helps maintain the high levels of ATP required for the calcification process [30]. In exchange, cnidarians afford inorganic nitrogen, phosphorus, and carbon, as well as a lighted environment that provides refuge from herbivores (**Figure 1**) [36, 37]. Signaling molecules regulating host-symbiont interaction have not been fully characterized. It has been suggested that translocation of photosynthetic products may be controlled by host release factors (HRFs) [30, 36], some of which are of proteinaceous nature (approximately 10 KDa) [38], although free amino acids and mycosporine-like amino acids have been found to induce the release of photosynthetically fixed carbon [39, 40].
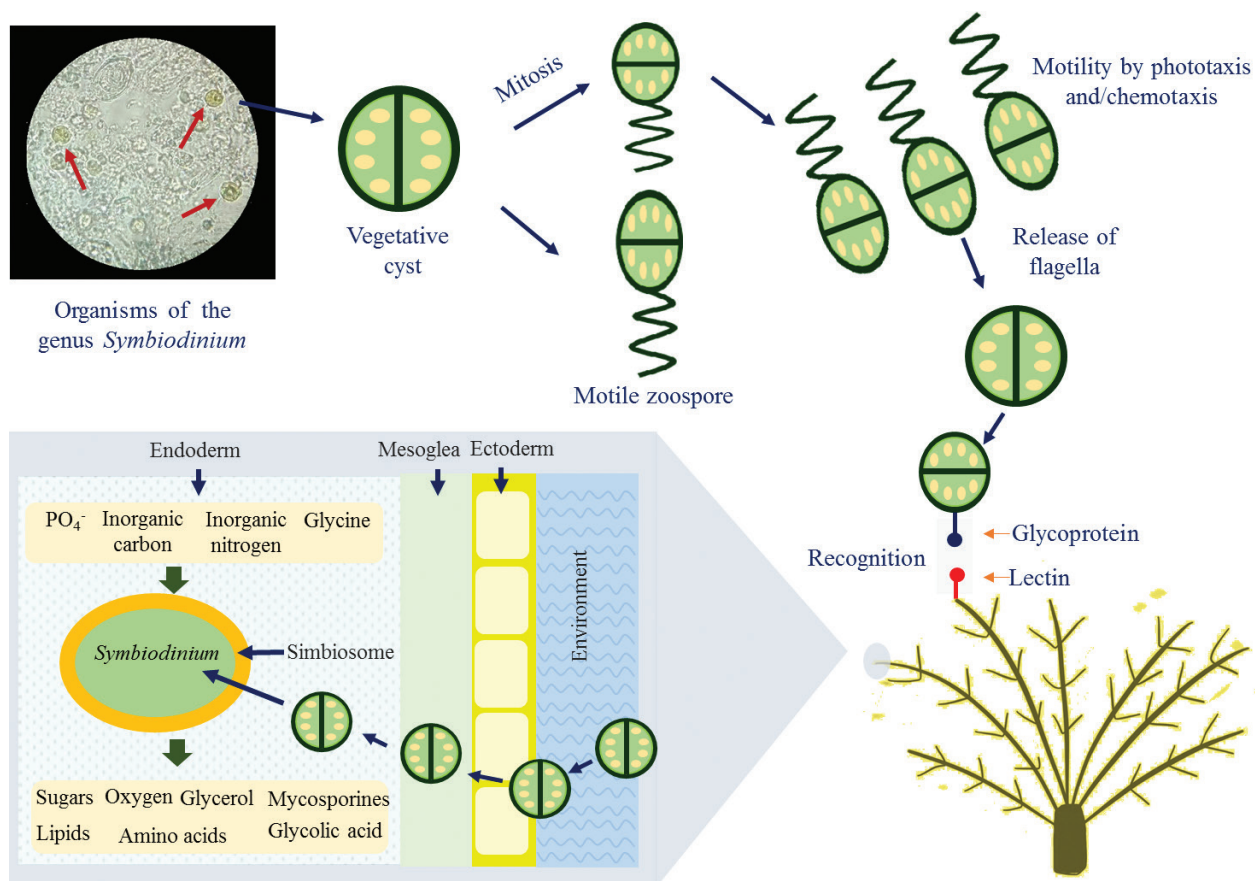
Figure 1. Cnidarian-*Symbiodinium* symbiosis.

Another important characteristic of reef-forming cnidarians is their capacity to produce calcified skeletons. Calcification is a crucial process for building the largest biological structures in the world [38, 41]. Despite its importance, the mechanism of calcification, or, more broadly, biomineralization, is little known. The coral exoskeleton is made of aragonite, a crystalline form of calcium carbonate ($CaCO_3$), and it is completely covered by a thin single layer of epithelial cells called calicoblastic epithelium (calicodermis). These cells play an important role in coral calcification, controlling the ionic composition of the medium in which calcification occurs (extracellular calcifying medium, ECM) [38, 41, 42].

Two hypotheses have been proposed to explain the stimulation of calcification by the presence of dinoflagellate symbionts [38]. One of them considers that absorption of CO_2 and release of O_2 by the symbionts [43] indirectly alter the pH and/or modify inorganic calcium concentration inside the gastrovascular cavity of the cnidarian, which leads to calcification by the precipitation of $CaCO_3$ [44]. The other hypothesis states that symbiotic algae produce organic molecules, such as nitrogenous compounds, glucose, and glycerol, that carry out the following functions: provide energy for calcification, modify the buffering capacity of the ECM, or are precursors for organic matrix synthesis [38, 45].

Colonies of reef-building cnidarians exhibit a great variety of colors due to the different types and concentrations of pigments conferred by the presence of the millions of symbionts

found per square centimeter in their tissues [46]. Symbionts can be acquired by either vertical or horizontal transmission. Vertical transmission occurs when symbionts are transferred from parents to offspring through direct inheritance. On the other hand, horizontally transmitted symbionts are acquired from the environment, such is the case of 80% of scleractinian symbiotic corals, whose larvae acquire their symbionts during a nutritional process [47–50]. The process of the establishment and maintenance of symbiosis comprises six phases: (i) initial contact; (ii) immersion of the symbiont; (iii) dynamic intracellular sorting of the symbionts; (iv) proliferation of symbionts in gastrodermal cells; (v) stabilization dynamics; and (vi) symbiosis dysfunction and breakdown [38]. According to some authors, the recognition of symbionts works in the same way as the recognition of pathogens, i.e., it involves pattern recognition receptors (PRRs) that are able to recognize and bind to specific conserved components of the cell walls of the algae (carbohydrates, lipids, and proteins) [51–53].

During their life cycle, *Symbiodinium* cells interchange between a vegetative cyst, which is the dominant form in the endosymbiotic state, and a motile zoospore that possesses thecal plates and two flagella, one transverse and one longitudinal [54]. The current hypothesis about the establishment of symbiosis between host cnidarians and *Symbiodinium* states that in the first phase, lectins, secreted by the host cell, induce symbionts to progress to cyst stage [30, 53]. Subsequently, lectins on the host cell surface attach to glycoproteins present on the surface of non-motile *Symbiodinium* cysts, which are subsequently phagocytized and carried into an early endocytic compartment by Rab5 proteins. Afterward, cells that were successfully recognized end up in a symbiosome, whereas damaged symbionts are digested by fusion with lysosomes after transiting through the late endocytic compartment. This traffic takes place through Rab7 and Rab11 proteins [30]. The relationship between cnidarians and symbiotic algae is regulated by environmental and physiological conditions of the host [30, 55].

It is clearly evident that establishment and maintenance of cnidarian-*Symbiodinium* symbiosis are critical to preserve homeostasis in coral reef ecosystems. On one side, algal symbionts obtain from their hosts protection and inorganic compounds, which are essential for their metabolism. On the other hand, cnidarians receive from their symbionts a great percentage of their energy demand and a balanced pH and precursor molecules needed for the calcification process. Undoubtedly, disruption of this symbiotic relationship can trigger numerous adverse effects, not only for the reef-forming organisms, but also for the great variety of organisms that depend on coral reefs.

3. Coral bleaching: causes and global episodes

Bleaching has been described as a visual effect of the stress that occurs when the symbiosis between reef-forming cnidarians and their symbiotic algae breaks down (**Figure 2**). It comprises the loss of pigmentation in coral reefs due to decreased *Symbiodinium* population, reduction in the concentration of their photosynthetic pigments, or both [12, 17, 56, 57]. Up to now, at least four general cellular mechanisms of algal loss have been proposed: *in situ*
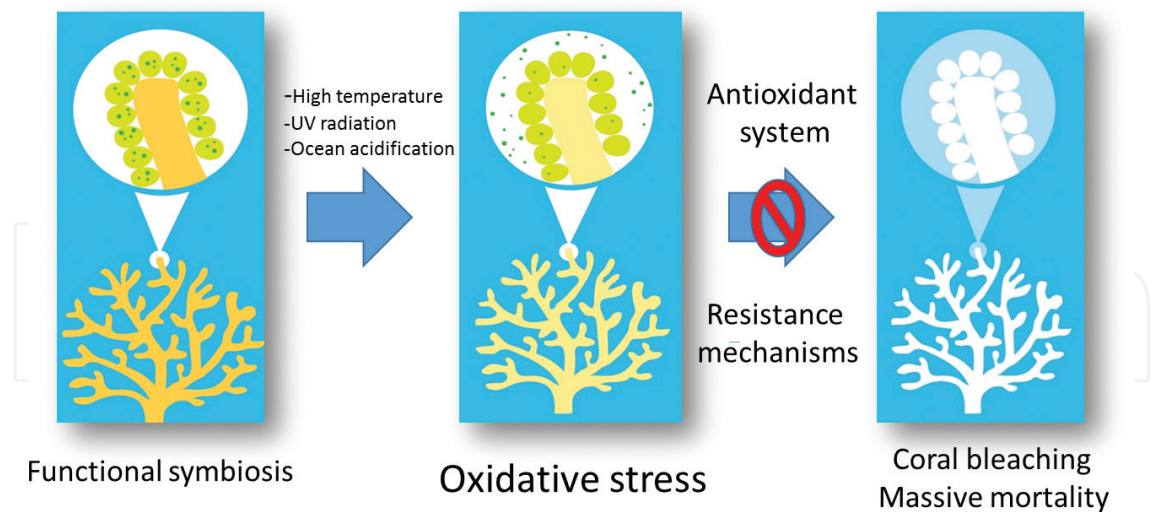
Figure 2. Coral reef bleaching. Modified from Baird et al. (2008) and http://oceanservice.noaa.gov/facts/coral_bleach.html.

degradation, symbiont (intact or degraded) expulsion, host-cell detachment, and host-cell death [58, 59].

It has been widely documented that several factors can induce coral bleaching, including reduced salinity [60]; amplified or reduced solar irradiation [61–64]; elevated [62, 65] or low water temperature [66, 67]; and the presence of chemical contaminants in the sea water, such as herbicides, pesticides, and cyanide [68]. However, field and laboratory investigations have indicated that elevated temperature is the principal cause of bleaching. Some of these studies are listed below.

(a) Hoegh-Guldberg and Smith (1989) studied the conditions required to achieve experimental bleaching of *Stylophora pistillata* and *Seriatopora hystrix*; they found that exposing fragments of these species to 32°C for 7 h caused a rate of expulsion of zooxanthellae 1000 times greater than in the control, which was kept at 27°C [62].

(b) Jokiel and Coles (1990) concluded that bleaching can be induced by short-term exposure (i.e., 1–2 days) to temperature increases of 3–4°C above normal summer temperature, or by long-term exposure (i.e., several weeks) to temperature increases of 1–2°C [66].

(c) Lesser et al. (1990) showed that increases in temperature significantly reduced the total number of zooxanthellae per polyp of the class Anthozoa. At the same time, temperature, solar radiation, and ultraviolet radiation independently increased the activities of superoxide dismutase (SOD), catalase, peroxidase, and ascorbate in the symbionts of *Palythoa caribaeorum* [69].

(d) Warner et al. (1999) sampled bleached colonies of *Montastraea faveolata* and *Montastraea franksi* in Florida. The bleaching was caused by a rise in temperature to over 30°C for 6 weeks during the summer of 1997. The analysis of these samples indicated damage in Photosystem II and a decrease in the expression of the D1 protein [70].

(e) Eakin et al. (2005) reported that the most serious bleaching event that affected Caribbean and Atlantic coral reefs happened in 2005, the warmest year ever documented in the Northern Hemisphere. Whitening of coral reefs provoked mortality of living reef-forming organisms by up to 40% [71].

Among the other environmental factors that can cause bleaching, besides thermal stress, solar radiation [17] has the most significant influence. This stressor can act independently of, or synergistically with, elevated sea water temperature [14, 72]. Fitt and Warner (1995) found a substantial reduction in symbiont photosynthesis in the coral *Montastraea annularis* after exposure to ultraviolet and blue light [73], whereas Gleason and Wellington (1993) demonstrated that bleaching occurred more readily when corals were exposed to high energy, short wavelength solar radiation [61]. Other studies have confirmed that exposure to high temperature and ultraviolet light exacerbates the stress on the symbiont population, contributing to bleaching [74, 75]. Along with increased temperature and high irradiance, elevated atmospheric CO_2 concentration is also affecting coral reefs by lowering ocean pH levels, which decreases calcification, increasing the rates of erosion that exceed the capacity for accretion of the reefs in tropical and subtropical zones [76–78].

Bleaching of coral reefs was first recorded in the 1870s [79, 80], and since 1980, coral reef bleaching and mortality episodes linked to elevated temperatures have been monitored. Ever since 1979, nine major coral bleaching episodes have affected coral reefs around the world, with an alarming rise in scale and frequency. At first, the phenomenon was regarded as linked to El Niño Southern Oscillation (ENSO) events [77, 81], which caused a high mortality in colonies of *Millepora platyphylla* in the Eastern Pacific coral reefs. However, since the early 1990s, it is known that bleaching is correlated in near real time with anomalously high satellite-derived sea surface temperature (SST) [81]. This relationship was clearly observed in the Caribbean basin during the 1980s and 1990s, when annual coral bleaching increased logarithmically with SST anomalies [82]. A minimal rise of only 0.1°C in regional SSTs caused a 35% increase in the extent and intensity of bleaching, while when SST was increased by 0.2°C and above, massive bleaching events took place [15].

The GCRMN (with support from more than 30 countries, the IOC-UNESCO, UNEP, IUCN, and the World Bank) has provided annual reports on the state of coral reefs. The report from 1997 to 1998 indicated the occurrence of an unprecedented global episode of mass coral bleaching. Before 1998, GCRMN surveys reported a 9.5% loss of corals in six regions. During 1998, one of the hottest years on record, these regions lost an average of 17.7% of their live reef-building corals [83]. The 1998 record was surpassed in 2005 and again in 2010 [71, 84]. However, 2014 [71, 85] and 2015 were considered the hottest years ever recorded, and 2016 continued this tendency, which has led to the longest and most damaging global coral bleaching event officially documented [86].

A summary of the major bleaching events reported since the 1980 is shown in **Table 1**. Unfortunately, anthropogenic activities that affect environment have provoked that coral bleaching events increase in frequency and severity, which represents a very serious threat to coral reefs worldwide. Reef-forming organisms have survived to mass extinction events in the past; however, it is unknown if they will be able to adapt fast enough to cope with rapid environmental change.

Date	Bleaching event
79/80	Great Barrier Reef
82/83	Eastern Pacific, Indonesia, Tokelau, Panama, Galapagos, Moorea, S-Japan
84	Moorea
86/87	Great Barrier Reef, Moorea, Caribbean Galapagos
88	Andaman Sea
89	Jamaica
90	Jamaica
91	Moorea, Andaman Sea
92/93	Great Barrier Reef, Galapagos
94	Pacific, E-Africa, Great Barrier Reef, Moorea
96	Arabian Gulf, Hawaii
97/98	**Worldwide**
00	South Africa, Easter Island
02	Great Barrier Reef, Arabian Gulf, Hawaii
05	Eastern Caribbean, Southern Africa
06	Great Barrier Reef
07	Iran
08/09	Queensland Australia
10	**Worldwide**
11	Western Australia Coast, Ningaloo Reef
15/16	**Worldwide**

Table 1. Documented bleaching events.

4. Molecular mechanisms underlying bleaching

It has been shown that, under elevated sea water temperatures and high solar radiation, *Symbiodinium* photosynthesis leads to intense oxidative stress in the two partners of the mutualistic symbiosis between reef-forming cnidarians and dinoflagellate endosymbionts [35, 87]. Oxidative stress involves the production and accumulation of reactive oxygen species (ROS), which can damage lipids, proteins, carbohydrates, and DNA [7, 52]. ROS play a key role in signal transduction of cell damage mediators and in processes such as apoptosis, autophagy, and necrosis [35, 88, 89]. In fact, numerous evidences indicate that the first step of bleaching involves inhibition of photosystem II (PSII) activity, a phenomenon referred to as photoinhibition, which often results in the overproduction of ROS, especially H_2O_2 [90, 91]. These cell damage response pathways are important during bleaching and depend on stress

intensity and duration [17, 35]. Moreover, it has been proposed that bleaching itself is a control mechanism to minimize the harmful effects caused by the metabolic imbalance in cnidarian-algal symbiosis [56].

Photosynthetic damage in *Symbiodinium* spp. has been proven using non-invasive chlorophyll fluorescence techniques, which demonstrated a significant loss of PSII photochemical efficiency during bleaching [70, 92, 93]. Elevated temperatures and high radiation cause photoinhibition and damage to the chloroplasts and the photosynthetic apparatus of the symbionts, through at least three pathways:

- Damage to the D1 protein, a core component of PSII, which is involved in the photolysis of water. This hypothesis proposes that, under stress conditions, the CO_2 fixation is limited and the electrons of PSI are transferred to O_2. This results in the formation of superoxide, which is quickly converted into H_2O_2 by superoxide dismutase (SOD). H_2O_2 hinders the repair of PSII by impairing the synthesis of the precursor D1 protein (pre-D1) [91]. During bleaching, the rate of photoinhibition and damage of D1 protein exceeds the rate of the PSII repair cycle [87].

- Inactivation of ribulose-1,5-bisphosphate carboxylase oxygenase (Rubisco), one of the key enzymes of the Calvin-Benzon cycle [94]. This mechanism was proposed when Bhagooli (2013) found that inhibition of the Calvin-Benson cycle by glycolaldehyde induced photoinhibition and coral bleaching, even at optimal temperatures [95].

- Injury of the thylakoidal membranes by ROS, which elicits an energy decoupling of the electron transport in both PSI and PSII, resulting in diminished ATP and NADP production [52]. The excess electrons reduce oxygen instead of NADPH with the subsequent generation of superoxide ion, which is reduced by SOD to H_2O_2. This last molecule reacts with ferrous ion and yields, the even more reactive, hydroxyl radical. Furthermore, excess electrons can react with photosynthetic pigments and molecular oxygen to produce atomic highly reactive oxygen. All the above-mentioned ROS spread to the host tissues triggering innate immunity, via the transcription factor NF-kB, leading to apoptosis [52]. Activation of NF-κB also induces iNOS expression, increasing the levels of nitric oxide, which reacts with superoxide ion to form peroxynitrite (ONOO-). This anion is highly reactive and damages the mitochondrial membrane, which releases pro-apoptotic molecules, such as AIF, promoting apoptosis (**Figure 3**) [96].

Another hypothesis to explain the molecular events that lead to bleaching proposes disruption to the carbon-concentrating mechanisms of the coral host. According to this hypothesis, bleaching is initiated by the inability of the coral to efficiently supply its symbionts with CO_2, mainly in periods of high solar radiation, when the algal CO_2 demand is very high. The lack of CO_2 needed for "dark reactions" reduces consumption of ATP and NADPH, blocking electron transport components. Sustained concentration of light excitation energy into the over-reduced electron transport chain triggers photoinhibition, damage to the photosynthetic components (mainly PSII), and ROS generation [97]. Excessive ROS production stimulates antioxidant defenses in the cnidarians and their symbionts, and it is also related to the exit of photosynthetic algae [98]. Moreover, bleaching can be caused by damage to "dark reactions" in the absence of thermal stress [99].
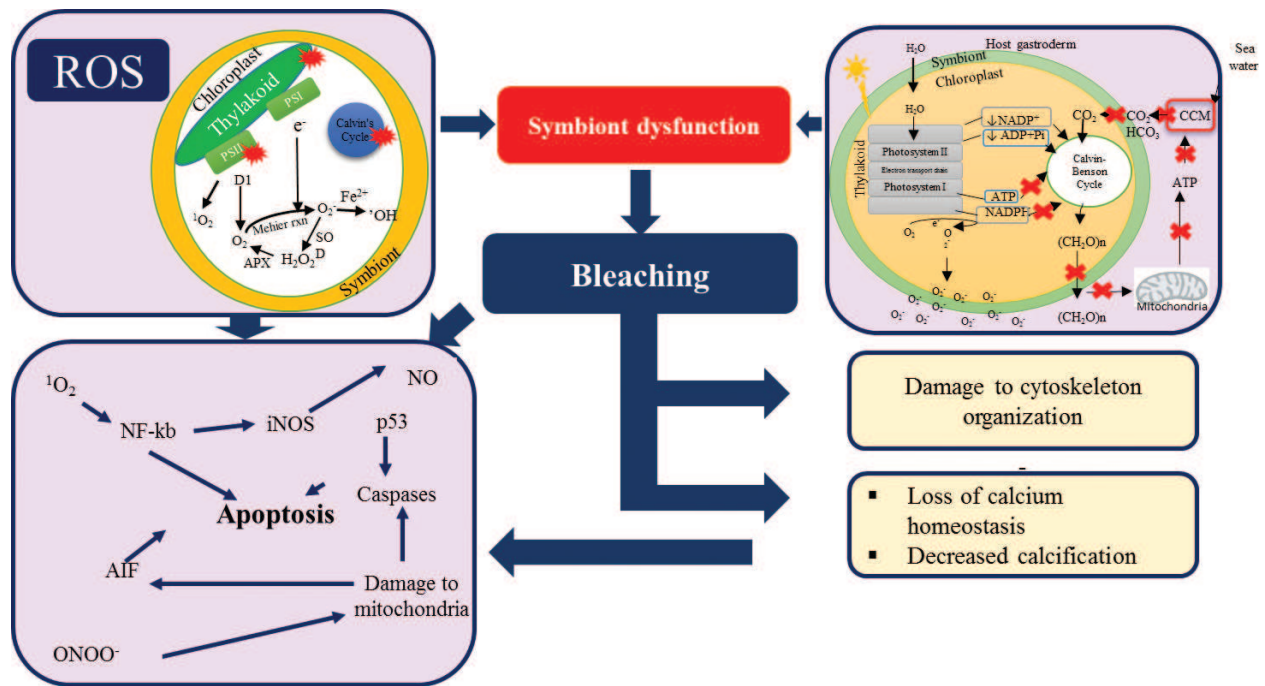
Figure 3. Molecular mechanisms of coral bleaching. Modified from Weis [52] and Wooldridge [98].

Recent investigations have examined the bleaching phenomenon employing genomic and transcriptomic approaches in order to measure changes in the expression of genes and transcripts during thermal stress and bleaching in different cnidarian species [100], including *Acropora nana* [21], *Stylophora pistillata* [22], *Acropora millepora* [101], *Acropora palmate* [24], *Aiptasia pallida* [25], *Orbicella faveolata* [23], and *Acropora hyacinthus* [27]. The results from those studies revealed that differential expression patterns occur between normal and bleached specimens, providing evidence that several important cell processes are affected by bleaching, such as stress response, Ca^{2+} homeostasis, cytoskeleton organization, cell transport, cell proliferation, apoptosis, calcification, protein expression, immune response, and metabolism, among others [21, 23–25, 27, 29, 101].

On the other hand, proteomic approaches have been applied to assess the effect of post-translational environmental stress on marine organisms [29. A recent study carried out on *Acropora palmata* showed that bleaching induced a differential protein expression response in this cnidarian. Thirty-eight key proteins were differentially expressed, primarily transcription factors involved in heat stress/UV responses, immunity, apoptosis, biomineralization, the cytoskeletal organization, and endo-exophagocytosis [24].

It is evident that up to now, the studies of climate-related stress on coral reefs have indicated that bleaching does not result from a single process, but rather from a complex interaction of environmental and genetic factors, operating at several levels within the reef-forming holobionts [99, 102, 103], which highlights the need for further detailed investigations directed toward a better understanding of the mechanisms underlying bleaching.

5. Mechanisms by which cnidarians face bleaching

Coral bleaching events have increased in frequency and intensity. Actually, some studies project that if this trend continues, tropical coral reefs might disappear this century [104, 105]. Mass coral bleaching and mortality events that have been registered worldwide over the past three decades have raised serious concerns about the future of coral reef ecosystems [77, 106]. Ecological extinction of corals reefs in some regions has been predicted to occur within the next 20–50 years, if reef-forming cnidarians are unable to adapt sufficiently rapidly to keep pace with global warming [107].

The ability to recover from a bleaching event has been associated with the energy reserves and heterotrophic feeding capacity of the cnidarian host [16, 108, 109]. *Symbiodinium* can provide up to 100% of a healthy coral's daily fixed carbon requirements; however, following bleaching, recovering corals may heavily rely on alternate sources of fixed carbon, which is acquired via catabolism of energy reserves and/or by increased heterotrophy [16, 110, 111].

Some evidences suggest that cnidarians are able to deal with thermal stress, through a series of adaptive processes (e.g., acclimatization, genetic adaptation, and symbiont shuffling), which may help reduce the harmful consequences and mortality provoked by bleaching [112, 113].

Acclimatization or acclimation is a type of phenotypic plasticity in which organisms, such as corals and their symbionts, can optimize their physiological performance in response to environmental changes [114]. The capacity for acclimation and adaptation of cnidarians and *Symbiodinium* clades is currently poorly known. Differentially expressed genes in *Acropora hyacinthus*, under physiological and stress conditions, suggested that the acclimatization that occurs less than 2 years after exposure to thermal stress is the same as that might have been expected from natural selection over many generations. Incorporating these adaptive capacities to ecosystem models will likely reduce the predictions of the disappearance of coral reef ecosystems [115].

Some studies have determined the existence of coral species that have survived high temperatures, indicating that they have higher thermal tolerance thresholds than others. Resistant species belong to the genera *Cyphastrea*, *Goniopora*, *Galaxea*, and *Pavona*, whereas species of the genera *Stylophora*, *Pocillopora*, and *Acropora* are more vulnerable to thermal stress [59]. In the case of *Symbiodinium* algae, some clades have been recognized as being more resistant than others. A study carried out on the major reef-building species in the Caribbean showed that *Symbiodinium* algae of the clade D display a significant thermal tolerance [116]. This was confirmed in a further study on *Orbicella faveolata* that demonstrated that under nonstressful conditions, thermally sensitive *Symbiodinium* of the clades B17 and C7 are prevalent, whereas after a bleaching event, clades D1 and A3 proliferated and repopulated cnidarian tissues previously evacuated by clades B17 and C7 [117].

Various mechanisms have been proposed to explain adaptive capacity of cnidarian species to face heat and radiation stress [7]. One of them involves photoprotection provided by pigments within the host tissues. Evidences supporting this proposal were obtained from a study of

the coral *Montipora monasteriata*, which was selected since it occurs in multiple color morphs (tan, blue, brown, green, and red). That study demonstrated that two of the non-fluorescent host pigments (CP-420 and CP-580) are up-regulated in response to elevated irradiance. This behavior appeared to favor retention of antennal chlorophyll by endosymbionts and therefore, photosynthetic capacity. It was found that up-regulated host pigments can facilitate the establishment of new or restructured dinoflagellate chloroplasts by modifying the internal light field. Particularly, high concentrations of CP-420 provided photoprotection for *Symbiodinium* by intercepting photons destined for photochemical quenching by dinoflagellate algae [118].

Another adaptive process entails non-photochemical quenching (NPQ) that dissipates excess light as heat. Reef corals produce fluorescent pigments belonging to a family related to green fluorescent proteins, which through the absorption, scattering, and dissipation of high-energy solar radiation by fluorescence reduce photoinhibition and the severity of bleaching [113]. Some of these sunscreen compounds are mycosporine-like amino acids, such as shinorine. This pigment showed no detectable fluorescence when excited at a frequency of 312–348 nm, which corresponds to the band of its mean-maximum absorption. Furthermore, electron paramagnetic resonance spectroscopy (EPR) revealed that purified shinorine (50 μM) produced no detectable radicals when irradiated with 305–700 nm. The lack of free radical formation by UV irradiation and the lack of fluorescence are consistent with the high efficiency dissipation of thermally absorbed UV energy [113, 119].

A well-known biochemical adaptation to thermal stress is the heat-shock response (HSR), which comprises the induced expression of a conserved set of molecular chaperones, known as heat-shock proteins. These molecules are critical for protein homeostasis, defense mechanisms, the refolding of denatured proteins, and the breakdown and replacement of non-replaceable proteins [120].

An additional adaptive response implies increased expression of enzymes that sequester oxygen radicals. The use of recent molecular techniques has improved our understanding of the magnitude of the transcriptional response of corals to various stressors, including high temperatures. An analysis carried out on *Acropora millepora* indicated that thermally stressed samples experienced a significant overexpression of four genes associated to cnidarian oxidative stress responses (HSP70, MnSOD, ferritin, and Zn^{2+}-metalloprotease) [121].

A caspase-mediated apoptotic cascade, caused by reactive oxygen species mainly generated by the algal symbionts, is a well-known factor that triggers bleaching and death of the host cnidarian. It has been shown that under high temperatures, some corals are able to naturally suppress caspase activity and significantly reduce caspase concentration as a mechanism to avoid colony death from apoptosis. It has been hypothesized that variability in response to thermal stress is determined by a four-element, combinatorial genetic matrix intrinsic to the specific symbiotic association [109].

On the other hand, symbiont shuffling and/or switching are considered other important mechanisms for explaining the way coral reef communities can counter environmental stress conditions. In some cases, the distribution of certain clades of *Symbiodinium* can substantially change after bleaching, via shuffling (a shift in symbiont dominance) or by symbiont switching (algae

are acquired from exogenous sources). A case study was performed on *Stylophora pistillata* that belonged to a coral reef that had suffered bleaching in March 2006. The objective of the study was to determine the percentages of different *Symbiodinium* clades populating the host after bleaching, and after the coral recovered from the event. Samples were collected in November 2006 and July 2007, and the results indicated the initial presence of clades C79, C78, C8/a, and C35/a, the last two in greater proportion. However, once the coral recovered from bleaching and repopulated, the proportions of C79, C35/a, and C78 decreased, while the population of C8/a increased considerably. Furthermore, other more resistant *Symbiodinium* clades appeared [122].

It is worth mentioning that studies directed toward understanding the causes and effects of bleaching, as well as the tolerance mechanisms that counteract this phenomenon have focused on Anthozoa species, showing that bleaching affects various processes that are essential to the survival of cnidarians. However, an integrative analysis is still needed to understand the molecular mechanisms underlying the different responses (adaptation or death) of cnidarians to coral bleaching.

6. Consequences of bleaching in coral reefs ecology

Undoubtedly, the bleaching phenomenon has seriously affected corals reefs. Although it has been observed that some reef-building cnidarians that suffer the loss of their symbiotic algae can, in some cases, survive and recover [90], bleaching can also lead to massive death [79, 104, 123], inflicting an enormous damage to the ecological balance of entire reef communities.

Coral reef monitoring programs exist in all regions of the world, recording reef features such as coral cover, fish biomass, and macroalgal cover, among others. However, at present the way of interpreting coral reef monitoring data has not been globally standardized, which hampers decision making directed toward protecting and rehabilitating coral reefs [124].

Several aspects regarding coral resistance and resilience are still unclear. For example, it is uncertain which *Symbiodinium* clades remain fairly viable following a stressful event and if they are able to significantly contribute to the recovery of bleached corals [30]. In this regard, some researchers reported that a majority of the expelled symbionts remained healthy, whereas others claimed that the survival of *Symbiodinium* did not last; some *Symbiodinium* cells, released into the water column after a thermal stress, had a drastically reduced photosynthetic activity after 5 days, suggesting that their survival could be compromised. Therefore, their contribution to the free-living stocks may be limited [125].

At present, coral resilience ability is the object of various research projects, since it has been widely documented that many corals that apparently recover from a bleaching event display a decrease in growth rate and calcification [114, 126], and are more susceptible to disease [127, 128], which is not surprising, since their supply of energy available for fundamental processes is diminished.

Gene expression biomarkers are emerging as powerful diagnosis tools for identifying and characterizing coral stress. Among the most plausible candidates are genes related to expression of heat-shock proteins, immune and oxidative stress responses, some metabolic

processes, and structural genes. Other genes, such as hsp16, Cacna1, MnSOD, SLC26, and Nf-kB, are showing excellent potential as reliable indicators of thermal stress in corals [107].

The impact on the reduction of the biodiversity of corals has not been fully envisaged. However, it is predicted that if reef-forming cnidarians do not evolve rapidly toward thermal tolerance, they will no longer dominate the reefs in the coming years [129, 130]. A possible scenario, according to some ecology specialists, is that if global warming continues at the present rate, a phase shift in coral reefs to an alternate state dominated by a different kind of organisms might occur [131, 132]. This alternate state might represent a substantial degradation of the coral reefs. Furthermore, degraded states can also be resilient to change, which complicates their possible reversal [11, 105].

7. Concluding remarks

Mass coral bleaching and mortality events that have been registered worldwide over the past three decades have raised serious concerns about the future of coral reef ecosystems. In fact, ecological extinction of corals reefs in some regions has been predicted to occur within the next 20–50 years, if reef-forming cnidarians are unable to adapt sufficiently rapidly to keep pace with global warming [104, 117, 133].

It is clear that the survival of coral reefs strongly depends on the functionality of the symbiosis between cnidarians and *Symbiodinium* algae, and up to now, we are just beginning to understand the molecular and cellular mechanisms underlying this relationship. Omics approaches have enabled a better comprehension about the way cnidarian-algal symbiosis functions and how holobiont physiology is modified by bleaching. Studies of the effects of global warming and coral bleaching have indicated that this event is the result of a complex interaction of environmental and genetic factors. Investigations of coral bleaching have also provided important insight into the mechanisms responsible for coral resistance to thermal stress.

It is evident that the key to understanding the future of coral reefs requires an insightful comprehension of the molecular and physiological mechanisms that promote thermal tolerance in the cnidarians and their symbionts, and to identify the genetic characteristics responsible for the variety of responses that occur in a coral bleaching event. Therefore, it is very important to continue studies in this regard to better understand cnidarian-*Symbiodinium* symbiosis, causes and effects of bleaching, the survival mechanisms of hosts and symbionts, as well as their ecological importance. Surely, the results derived from these studies will be useful to design strategies and policies to restore coral reefs and to promote their conservation.

Acknowledgements

Appendix

Acronyms	Definition
IOC	Intergovernmental Oceanographic Commission
UNESCO	United Nations Educational, Scientific and Cultural Organization
UNEP	United Nations Environment Programme
IUCN	International Union for Conservation of Nature
HRFs	Host release factors
ECM	Extracellular calcifying medium
PRRs	Pattern recognition receptors
UV	Ultraviolet radiation
SST	Sea surface temperature
ENSO	El Nino Southern Oscillation
GCRMN	The Global Coral Reef Monitoring Network
PSII	Photosystem II
ROS	Reactive oxygen species
RuBisCO	Ribulose-1,5-bisphosphate carboxylase oxygenase enzyme
SOD	Superoxide dismutase enzyme
PSI	Photosystem I
AIF	*Apoptosis-inducing factor*
NPQ	Non-photochemical quenching
EPR	Paramagnetic resonance spectroscopy
HSR	Heat-shock response
APX	Catalase
NADPH	Nicotinamide adenine dinucleotide phosphate
NF-KB	Nuclear factor kappa-light-chain-enhancer of activated B cells
p53	p53-gen

Author details

Norma Olguín-López, Carolina Gutiérrez-Chávez, Víctor Hugo Hérnández-Elizárraga, César Ibarra-Alvarado and Alejandra Rojas-Molina*

*Address all correspondence to: rojasa@uaq.mx

School of Chemistry, Autonomous University of Querétaro, Santiago de Querétaro, México

References

[1]   Anthony KR. Ecosystem Damages from Loss of Coral Reefs Under Climate Change. Annu Rev Environ Resour. 2016;**41**:59-81

[2]   Williams SM, Sánchez-Godínez C, Newman SP, Cortés J. Ecological assessments of the coral reef communities in the Eastern Caribbean and the effects of herbivory in influencing coral juvenile density and algal cover. Mar Ecol. 2017;**38**:e12395

[3]   Roth MS. The engine of the reef: photobiology of the coral-algal symbiosis. Front Microbiol. 2014;**5**:422

[4]   Rogers CS, Miller J. Measuring, Interpreting, and Responding to Changes in Coral Reefs: A Challenge for Biologists, Geologists, and Managers. Coral Reefs at the Crossroads. Springer Netherlands. 2016;277-92

[5]   Jain R, Sonawane S, Mandrekar N. Marine organisms: Potential source for drug discovery. Curr Sci-Bangalore-. 2008;**94**(3):292

[6]   Cragg GM, Newman DJ. Natural products: a continuing source of novel drug leads. Biochim Biophys Acta. 2013;**1830**(6):3670-95

[7]   Baird AH, Bhagooli R, Ralph PJ, Takahashi S. Coral bleaching: the role of the host. Trends Ecol Evol. 2009;**24**(1):16-20

[8]   Lesser MP. Coral reef bleaching and global climate change: Can corals survive the next century? Proc Natl Acad Sci. 2007;**104**(13):5259-5260

[9]   Lough JM. Coral reefs: Turning back time. Nature. 2016;**531**(7594):314-315

[10] Mumby PJ, Van Woesik R. Consequences of ecological, evolutionary and biogeochemical uncertainty for coral reef responses to climatic stress. Curr Biol. 2014;**24**(10):R413-R423

[11] Mora C, Graham NAJ, Nyström M. Ecological limitations to the resilience of coral reefs. Coral Reefs. 2016;**35**(4):1271-80

[12] Lesser MP. Oxidative stress in marine environments: biochemistry and physiological ecology. Annu Rev Physiol. 2006;**68**:253-278

[13] Ainsworth TD, Hoegh-Guldberg O, Heron SF, Skirving WJ, Leggat W. Early cellular changes are indicators of pre-bleaching thermal stress in the coral host. J Exp Mar Biol Ecol. 2008;**364**(2):63-71

[14] Brown BE, Dunne RP. Coral Bleaching: The Roles of Sea Temperature and Solar Radiation. ResearchGate. 2015;**99**(C10):266-83

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

[16] Grottoli AG, Warner ME, Levas SJ, Aschaffenburg MD, Schoepf V, McGinley M, et al. The cumulative impact of annual coral bleaching can turn some coral species winners into losers. Glob Change Biol. 2014;**20**(12):3823-3833

[17] Lesser MP. Coral bleaching: causes and mechanisms. In: Coral reefs: an ecosystem in transition. Springer Netherlands. 2011:405-419

[18] Okazaki RR, Towle EK, van Hooidonk R, Mor C, Winter RN, Piggot AM, et al. Species-specific responses to climate change and community composition determine future calcification rates of Florida Keys reefs. Glob Change Biol. 2016;**23**(3):1023-1035

[19] van Hooidonk R, Maynard JA, Manzello D, Planes S. Opposite latitudinal gradients in projected ocean acidification and bleaching impacts on coral reefs. Glob Change Biol. 2014;**20**(1):103-12

[20] Jackson J, Donovan M, Cramer K, Lam V. Status and trends of Caribbean coral reefs: 1970-2012 Global Coral Reef Monitoring Network, International Union for the Conservation of Nature Global Marine and Polar Program, Washington, DC

[21] Bay RA, Palumbi SR. Rapid acclimation ability mediated by transcriptome changes in reef-building corals. Genome Biol Evol. 2015;**7**(6):1602-1612

[22] Maor-Landaw K, Levy O. Gene expression profiles during short-term heat stress; branching vs. massive Scleractinian corals of the Red Sea. Peer J. 2016;**4**:e1814

[23] Pinzón JH, Kamel B, Burge CA, Harvell CD, Medina M, Weil E, et al. Whole transcriptome analysis reveals changes in expression of immune-related genes during and after bleaching in a reef-building coral. R Soc Open Sci. 2015;**2**(4):140214

[24] Ricaurte M, Schizas NV, Ciborowski P, Boukli NM. Proteomic analysis of bleached and unbleached *Acropora palmata*, a threatened coral species of the Caribbean. Mar Pollut Bull. 2016;**107**(1):224-232

[25] Sloan R, Sawyer S. The role of cellular signaling during bleaching in the sea anemone, *Aiptasia pallida*. Proc W Va Acad Sci. 2016;**88**:1

[26] DeSalvo MK, Estrada A, Sunagawa S, Medina M. Transcriptomic responses to darkness stress point to common coral bleaching mechanisms. Coral Reefs. 2012;**31**(1):215-228

[27] Seneca FO, Palumbi SR. The role of transcriptome resilience in resistance of corals to bleaching. Mol Ecol. 2015;**24**(7):1467-1484

[28] Anderson DA, Walz ME, Weil E, Tonellato P, Smith MC. RNA-Seq of the Caribbean reef-building coral *Orbicella faveolata* (Scleractinia-Merulinidae) under bleaching and disease stress expands models of coral innate immunity. Peer J. 2016;**4**:e1616

[29] Tomanek L. Environmental Proteomics: Changes in the Proteome of Marine Organisms in Response to Environmental Stress, Pollutants, Infection, Symbiosis, and Development. Annu Rev Mar Sci. 2011;**3**(1):373-99

[30] Fransolet D, Roberty S, Plumier JC. Establishment of endosymbiosis: The case of cnidarians and Symbiodinium. J Exp Mar Biol Ecol. 2012;**420**:1-7

[31] Baker AC, Correa AMS, Cunning R. Diversity, Distribution and Stability of Symbiodinium in Reef Corals of the Eastern Tropical Pacific. Coral Reefs of the Eastern Tropical Pacific. Springer Netherlands; 2017;405-20

[32] Yellowlees D, Rees TAV, Leggat W. Metabolic interactions between algal symbionts and invertebrate hosts. Plant Cell Environ. 2008;**31**(5):679-694

[33] Baghdasarian G, Muscatine L. Preferential expulsion of dividing algal cells as a mechanism for regulating algal-cnidarian symbiosis. Biol Bull. 2000;**199**(3):278-86

[34] Dimond J, Carrington E. Symbiosis regulation in a facultatively symbiotic temperate coral: zooxanthellae division and expulsion. Coral Reefs. 2008;**27**(3):601-604

[35] Muller-Parker G, D'Elia CF, Cook CB. Interactions between corals and their symbiotic algae. In: Coral Reefs in the Anthropocene. Springer Netherlands. 2015:99-116

[36] Venn AA, Loram JE, Douglas AE. Photosynthetic symbioses in animals. J Exp Bot. 2008;**59**(5):1069-1080

[37] Yellowlees D, Rees TAV, Leggat W. Metabolic interactions between algal symbionts and invertebrate hosts. Plant Cell Environ. 2008;**31**(5):679-694

[38] Davy SK, Allemand D, Weis VM. Cell biology of cnidarian-dinoflagellate symbiosis. Microbiol Mol Biol Rev. 2012;**76**(2):229-261

[39] Biel KY, Gates RD, Muscatine L. Effects of free amino acids on the photosynthetic carbon metabolism of symbiotic dinoflagellates. Russ J Plant Physiol. 2007;**54**(2):171-83

[40] Cook CB, Davy SK. Are free amino acids responsible for the `host factor' effects on symbiotic zooxanthellae in extracts of host tissue? Hydrobiologia. 2001;**461**(1-3):71-8

[41] Osinga R, Schutter M, Griffioen B, Wijffels RH, Verreth JAJ, Shafir S, et al. The Biology and Economics of Coral Growth. Mar Biotechnol N Y N. 2011;**13**(4):658-71

[42] Muscatine L, Tambutte E, Allemand D. Morphology of coral desmocytes, cells that anchor the calicoblastic epithelium to the skeleton. Coral Reefs. 1997;**16**(4):205-213

[43] Furla P, Bénazet-Tambutté S, Jaubert J, Allemand D. Functional polarity of the tentacle of the sea anemone *Anemonia viridis*: role in inorganic carbon acquisition. Am J Physiol. 1998;**274**(2 Pt 2):R303-310

[44] Venn A, Tambutté E, Holcomb M, Allemand D, Tambutté S. Live Tissue Imaging Shows Reef Corals Elevate pH under Their Calcifying Tissue Relative to Seawater. PLoS ONE. 2011;**6**(5):e20013

[45] Colombo-Pallotta MF, Rodríguez-Román A, Iglesias-Prieto R. Calcification in bleached and unbleached *Montastraea faveolata*: evaluating the role of oxygen and glycerol. Coral Reefs. 2010;**29**(4):899-907

[46] Oswald F, Schmitt F, Leutenegger A, Ivanchenko S, D'Angelo C, Salih A, et al. Contributions of host and symbiont pigments to the coloration of reef corals. FEBS J. 2007;**274**(4):1102-9

[47] Fabricius KE, Mieog JC, Colin PL, Idip D, H Van Oppen M. Identity and diversity of coral endosymbionts (zooxanthellae) from three Palauan reefs with contrasting bleaching, temperature and shading histories. Mol Ecol. 2004;**13**(8):2445-2458

[48] Mauricio R-L, Wendy P, Virginia W. Transcriptome analysis of a cnidarian-dinoflagellate mutualism reveals complex modulation of host gene expression. Bmc genomics. 2006;**7**(1):23

[49] Schwarz JA, Krupp DA, Weis VM. Late larval development and onset of symbiosis in the scleractinian coral *Fungia scutaria*. Biol Bull. 1999;**196**(1):70-79

[50] Weis VM, Reynolds WS, Krupp DA, others. Host-symbiont specificity during onset of symbiosis between the dinoflagellates *Symbiodinium spp*. and planula larvae of the scleractinian coral Fungia scutaria. Coral Reefs. 2001;**20**(3):301-308

[51] Logan DDK, LaFlamme AC, Weis VM, Davy SK. Flow-Cytometric Characterization of the Cell-Surface Glycans of Symbiotic Dinoflagellates (*Symbiodinium spp*.). J Phycol. 2010;**46**(3):525-33

[52] Weis VM. Cellular mechanisms of Cnidarian bleaching: stress causes the collapse of symbiosis. J Exp Biol. 2008;**211**(19):3059-3066

[53] Wood-Charlson EM, Hollingsworth LL, Krupp DA, Weis VM. Lectin/glycan interactions play a role in recognition in a coral/dinoflagellate symbiosis. Cell Microbiol. 2006;**8**(12):1985-93

[54] Freudenthal HD. *Symbiodinium* gen. nov. and *Symbiodinium microadriaticum* sp. nov., a Zooxanthella: Taxonomy, Life Cycle, and Morphology. J Protozool. 1962;**9**(1):45-52

[55] Jones AM, Berkelmans R, van Oppen MJ, Mieog JC, Sinclair W. A community change in the algal endosymbionts of a scleractinian coral following a natural bleaching event: field evidence of acclimatization. Proc R Soc B Biol Sci. 2008;**275**(1641):1359-1365

[56] Obura DO. Reef corals bleach to resist stress. Mar Pollut Bull. 2009;**58**(2):206-212

[57] Hoegh-Guldberg O. Climate change, coral bleaching and the future of the world's coral reefs. Mar Freshw Res. 1999;**50**(8):839-866

[58] Jokiel PL, Coles SL. Response of Hawaiian and other Indo-Pacific reef corals to elevated temperature. Coral Reefs. 1990;**8**(4):155-162

[59] McClanahan TR, Baird AH, Marshall PA, Toscano MA. Comparing bleaching and mortality responses of hard corals between southern Kenya and the Great Barrier Reef, Australia. Mar Pollut Bull. 2004;**48**(3):327-335

[60] Al-Naema N, Deb N, Saeed S, Dupont J, Ben-Hamadou R. Acute orthogonal stress driven by temperature, salinity and light intensity on Qatari Porites photosynthesis and growth. Qscience Proc. 2015;(5):17

[61] Gleason DF, Wellington GM. Ultraviolet radiation and coral bleaching. Nature. 1993;**365**(6449):836-838

[62] Hoegh-Guldberg O, Smith GJ. The effect of sudden changes in temperature, light and salinity on the population density and export of zooxanthellae from the reef corals *Stylophora pistillata* Esper and *Seriatopora hystrix* Dana. J Exp Mar Biol Ecol. 1989;**129**(3):279-303

[63] Lesser MP, Farrell JH. Exposure to solar radiation increases damage to both host tissues and algal symbionts of corals during thermal stress. Coral Reefs. 2004;**23**(3):367-377

[64] Yonge CM. The significance of the relationship between corals and zooxanthellae. Nature. 1931;**128**:309-311

[65] Glynn PW, D'croz L. Experimental evidence for high temperature stress as the cause of El Niño-coincident coral mortality. Coral Reefs. 1990;**8**(4):181-191

[66] Jokiel PL, Coles SL. Effects of temperature on the mortality and growth of Hawaiian reef corals. Mar Biol. 1977;**43**(3):201-208

[67] Steen RG, Muscatine L. Low temperature evokes rapid exocytosis of symbiotic algae by a sea anemone. Biol Bull. 1987;**172**(2):246-263

[68] Hoegh-Guldberg O, Jones RJ. Photoinhibition and photoprotection in symbiotic dinoflagellates from reef-building corals. Mar Ecol Prog Ser. 1999;**183**:73-86

[69] Lesser MP, Stochaj WR, Tapley DW, Shick JM. Bleaching in coral reef anthozoans: effects of irradiance, ultraviolet radiation, and temperature on the activities of protective enzymes against active oxygen. Coral Reefs. 1990;**8**(4):225-232

[70] Warner ME, Fitt WK, Schmidt GW. Damage to photosystem II in symbiotic dinoflagellates: a determinant of coral bleaching. Proc Natl Acad Sci. 1999;**96**(14):8007-8012

[71] Eakin CM, Morgan JA, Heron SF, Smith TB, Liu G, Alvarez-Filip L, et al. Caribbean corals in crisis: record thermal stress, bleaching, and mortality in 2005. PloS One. 2010;**5**(11):e13969

[72] Ban SS, Graham NAJ, Connolly SR. Evidence for multiple stressor interactions and effects on coral reefs. Glob Change Biol. 2014;**20**(3):681-97

[73] Fitt WK, Warner ME. Bleaching patterns of four species of Caribbean reef corals. Biol Bull. 1995;**189**(3):298-307

[74] Courtial L, Roberty S, Shick JM, Houlbrèque F, Ferrier-Pagès C. Interactive effects of ultraviolet radiation and thermal stress on two reef-building corals. Limnol Oceanogr. 2017;**62**(3):1000-13

[75] Drohan AF, Thoney DA, Baker AC. Synergistic effect of high temperature and ultraviolet-B radiation on the gorgonian *Eunicea tourneforti* (Octocorallia: Alcyonacea: Plexauridae). Bull Mar Sci. 2005;**77**(2):257-66

[76] Anthony KRN, Kline DI, Diaz-Pulido G, Dove S, Hoegh-Guldberg O. Ocean acidification causes bleaching and productivity loss in coral reef builders. Proc Natl Acad Sci. 2008;**105**(45):17442-6

[77] Hoegh-Guldberg O, Mumby PJ, Hooten AJ, Steneck RS, Greenfield P, Gomez E, et al. Coral reefs under rapid climate change and ocean acidification. Science. 2007; **318**(5857):1737-1742

[78] Pandolfi JM, Connolly SR, Marshall DJ, Cohen AL. Projecting coral reef futures under global warming and ocean acidification. Science. 2011;**333**(6041):418-22

[79] Brown BE. Coral bleaching: causes and consequences. Coral Reefs. 1997;**16**(1):S129-S138

[80] Glynn PW. Coral reef bleaching: ecological perspectives. Coral Reefs. 1993;**12**(1):1-17

[81] Goreau TJ, Hayes RL, McAlllister D. Regional patterns of sea surface temperature rise: implications for global ocean circulation change and the future of coral reefs and fisheries. World Resour Rev. 2005;**17**(3):350-370

[82] McWilliams JP, Côté IM, Gill JA, Sutherland WJ, Watkinson AR. Accelerating impacts of temperature-induced coral bleaching in the Caribbean. Ecology. 2005;**86**(8):2055-2060

[83] Hoegh-Guldberg O, Bruno JF. The impact of climate change on the world's marine ecosystems. Science. 2010;**328**(5985):1523-1528

[84] Alemu JB, Clement Y, others. Mass coral bleaching in 2010 in the southern Caribbean. PLoS One. 2014;**9**(1):e83829

[85] Mann ME, Rahmstorf S, Steinman BA, Tingley M, Miller SK. The likelihood of recent record warmth. Sci Rep. 2016;**6**:19831

[86] Heron SF, Maynard JA, van Hooidonk R, Eakin CM. Warming Trends and Bleaching Stress of the World's Coral Reefs 1985-2012. Sci Rep. 2016;**6**:38402

[87] Hill R, Brown CM, DeZeeuw K, Campbell DA, Ralph PJ. Increased rate of D1 repair in coral symbionts during bleaching is insufficient to counter accelerated photo-inactivation. Limnol Oceanogr. 2011;**56**(1):139-46

[88] Ross C, Ritson-Williams R, Olsen K, Paul VJ. Short-term and latent post-settlement effects associated with elevated temperature and oxidative stress on larvae from the coral *Porites astreoides*. Coral Reefs. 2013;**32**(1):71-79

[89] Yakovleva IM, Baird AH, Yamamoto HH, Bhagooli R, Nonaka M, Hidaka M. Algal symbionts increase oxidative damage and death in coral larvae at high temperatures. Mar Ecol Prog Ser. 2009;**378**:105-112

[90] Hume B, D'Angelo C, Burt J, Baker AC, Riegl B, Wiedenmann J. Corals from the Persian/Arabian Gulf as models for thermotolerant reef-builders: Prevalence of clade C3 *Symbiodinium*, host fluorescence and *ex situ* temperature tolerance. Mar Pollut Bull. 2013;**72**(2):313-322

[91] Takahashi S, Murata N. How do environmental stresses accelerate photoinhibition? Trends Plant Sci. 2008;**13**(4):178-182

[92] Hill R, Schreiber U, Gademann R, Larkum AW, Kühl M, Ralph PJ. Spatial heterogeneity of photosynthesis and the effect of temperature-induced bleaching conditions in three species of corals. Mar Biol. 2004;**144**(4):633-640

[93] Jones RJ, Hoegh-Guldberg O, Larkum AWD, Schreiber U. Temperature-induced bleaching of corals begins with impairment of the CO2 fixation mechanism in zooxanthellae. Plant Cell Environ. 1998;**21**(12):1219-30

[94]   Lilley RM, Ralph PJ, Larkum AWD. The determination of activity of the enzyme Rubisco in cell extracts of the dinoflagellate alga *Symbiodinium* sp. by manganese chemiluminescence and its response to short-term thermal stress of the alga. Plant Cell Environ. 2010;**33**(6):995-1004

[95]   Bhagooli R. Inhibition of Calvin-Benson cycle suppresses the repair of photosystem II in *Symbiodinium*: implications for coral bleaching. Hydrobiologia. 2013;**714**(1):183-90

[96]   Perez S, Weis V. Nitric oxide and cnidarian bleaching: an eviction notice mediates breakdown of a symbiosis. J Exp Biol. 2006;**209**(14):2804-2810

[97]   Hill R, Szabó M, ur Rehman A, Vass I, Ralph PJ, Larkum AWD. Inhibition of photosynthetic CO_2 fixation in the coral *Pocillopora damicornis* and its relationship to thermal bleaching. J Exp Biol. 2014;**217**(Pt 12):2150-62

[98]   Wooldridge SA. Breakdown of the coral-algae symbiosis: towards formalising a linkage between warm-water bleaching thresholds and the growth rate of the intracellular zooxanthellae. Biogeosciences. 2013;**10**(3):1647-1658

[99]   Tolleter D, Seneca FO, DeNofrio JC, Krediet CJ, Palumbi SR, Pringle JR, et al. Coral bleaching independent of photosynthetic activity. Curr Biol CB. 2013;**23**(18):1782-6

[100]   Maor-Landaw K, Levy O. Survey of Cnidarian Gene Expression Profiles in Response to Environmental Stressors: Summarizing 20 Years of Research, What Are We Heading for? In: The Cnidaria, Past, Present and Future. Springer Netherlands. 2016:523-543

[101]   Raina JB, Lutz A, Motti CA, Miller DJ, van Oppen MJH. Host Coenzyme Q Redox State Is an Early Biomarker of Thermal Stress in the Coral *Acropora millepora*. PLOS ONE. 2015;**10**(10):e0139290

[102]   Buxton L, Takahashi S, Hill R, Ralph PJ. Variability in the primary site of photosynthetic damage in *Symbiodinium sp.*(dinophyceae) exposed to thermal stress1. J Phycol. 2012;**48**(1):117-126

[103]   Bieri T, Onishi M, Xiang T, Grossman AR, Pringle JR. Relative Contributions of Various Cellular Mechanisms to Loss of Algae during Cnidarian Bleaching. PLOS ONE. 2016;**11**(4):e0152693

[104]   Hoegh-Guldberg O, Poloczanska ES, Skirving W, Dove S. Coral Reef Ecosystems under Climate Change and Ocean Acidification. Front Mar Sci. 2017;**4**:158

[105]   Logan CA, Dunne JP, Eakin CM, Donner SD. Incorporating adaptive responses into future projections of coral bleaching. Glob Change Biol. 2014;**20**(1):125-39

[106]   Hughes TP, Baird AH, Bellwood DR, Card M, Connolly SR, Folke C, et al. Climate change, human impacts, and the resilience of coral reefs. science. 2003;**301**(5635):929-933

[107]   Louis YD, Bhagooli R, Kenkel CD, Baker AC, Dyall SD. Gene expression biomarkers of heat stress in scleractinian corals: Promises and limitations. Comp Biochem Physiol Part C Toxicol Pharmacol. 2017;**191**:63-77

[108] Levas S, Grottoli AG, Schoepf V, Aschaffenburg M, Baumann J, Bauer JE, et al. Can heterotrophic uptake of dissolved organic carbon and zooplankton mitigate carbon budget deficits in annually bleached corals? Coral Reefs. 2016;**35**(2):495-506

[109] Tchernov D, Kvitt H, Haramaty L, Bibby TS, Gorbunov MY, Rosenfeld H, et al. Apoptosis and the selective survival of host animals following thermal bleaching in zooxanthellate corals. Proc Natl Acad Sci. 2011;**108**(24):9905-9909

[110] Aichelman HE, Townsend JE, Courtney TA, Baumann JH, Davies SW, Castillo KD. Heterotrophy mitigates the response of the temperate coral *Oculina arbuscula* to temperature stress. Ecol Evol. 2016;**6**(18):6758-69

[111] Tremblay P, Gori A, Maguer JF, Hoogenboom M, Ferrier-Pagès C. Heterotrophy promotes the re-establishment of photosynthate translocation in a symbiotic coral after heat stress. Sci Rep. 2016;**6**:srep38112

[112] Ainsworth TD, Heron SF, Ortiz JC, Mumby PJ, Grech A, Ogawa D, et al. Climate change disables coral bleaching protection on the Great Barrier Reef. Science. 2016;**352**(6283):338-42

[113] Salih A, Cox G, Szymczak R, Coles SL, Baird AH, Dunstan A, et al. The role of host-based color and fluorescent pigments in photoprotection and in reducing bleaching stress in corals. In: Proc 10th Int Coral Reef Symp. 2006:746-756

[114] Coles SL, Brown BE. Coral bleaching-capacity for acclimatization and adaptation. Adv Mar Biol. 2003;**46**:183-223

[115] Palumbi SR, Barshis DJ, Traylor-Knowles N, Bay RA. Mechanisms of reef coral resistance to future climate change. Science. 2014;**344**(6186):895-898

[116] LaJeunesse TC, Smith RT, Finney J, Oxenford H. Outbreak and persistence of opportunistic symbiotic dinoflagellates during the 2005 Caribbean mass coral 'bleaching' event. Proc R Soc Lond B Biol Sci. 2009;**276**(1676):4139-48

[117] Kemp DW, Hernandez-Pech X, Iglesias-Prieto R, Fitt WK, Schmidt GW. Community dynamics and physiology of *Symbiodinium spp*. before, during, and after a coral bleaching event. Limnol Oceanogr. 2014;**59**(3):788-797

[118] Dove SG, Lovell C, Fine M, Deckenback J, Hoegh-Guldberg O, Iglesias-Prieto R, et al. Host pigments: potential facilitators of photosynthesis in coral symbioses. Plant Cell Environ. 2008;**31**(11):1523-1533

[119] Shick JM, Dunlap WC. Mycosporine-like amino acids and related gadusols: biosynthesis, accumulation, and UV-protective functions in aquatic organisms. Annu Rev Physiol. 2002;**64**(1):223-262

[120] Hofmann GE, Todgham AE. Living in the now: physiological mechanisms to tolerate a rapidly changing environment. Annu Rev Physiol. 2010;**72**:127-145

[121] Császár NBM, Seneca FO, Van Oppen MJH. Variation in antioxidant gene expression in the scleractinian coral *Acropora millepora* under laboratory thermal stress. Mar Ecol Prog Ser. 2009;**392**:93-102

[122] Sampayo EM, Ridgway T, Bongaerts P, Hoegh-Guldberg O. Bleaching susceptibility and mortality of corals are determined by fine-scale differences in symbiont type. Proc Natl Acad Sci. 2008;**105**(30):10444-10449

[123] Banaszak AT. Photoprotective physiological and biochemical responses of aquatic organisms. UV Eff Aquat Org Ecosyst. 2003;329-356

[124] Flower J, Ortiz JC, Chollett I, Abdullah S, Castro-Sanguino C, Hock K, et al. Interpreting coral reef monitoring data: A guide for improved management decisions. Ecol Indic. 2017;**72**:848-69

[125] Hill R, Ralph P. Post-bleaching viability of expelled zooxanthellae from the scleractinian coral *Pocillopora damicornis*. ýMar. Ecol. Prog. Ser. 2007;**352**:137-144

[126] Foster T, Short JA, Falter JL, Ross C, McCulloch MT. Reduced calcification in Western Australian corals during anomalously high summer water temperatures. J Exp Mar Biol Ecol. 2014;**461**:133-43

[127] Maynard J, van Hooidonk R, Eakin CM, Puotinen M, Garren M, Williams G, et al. Projections of climate conditions that increase coral disease susceptibility and pathogen abundance and virulence. Nat Clim Change. 2015;**5**(7):688-94

[128] Rosenberg E, Koren O, Reshef L, Efrony R, Zilber-Rosenberg I. The role of microorganisms in coral health, disease and evolution. Nat Rev Microbiol. 2007;**5**(5):355-362

[129] Pandolfi JM. Incorporating Uncertainty in Predicting the Future Response of Coral Reefs to Climate Change. Annu Rev Ecol Evol Syst. 2015;**46**(1):281-303

[130] Wild C H-GO, Loya Y, Bythell J, Fitt W, Gates R, Iglesias-Prieto R, et al. Bleaching and Relate Ecological Factors. Melbourne, Australia. Ed. Currie Communications; 2009

[131] Cheal AJ, MacNeil MA, Cripps E, Emslie MJ, Jonker M, Schaffelke B, et al. Coral-macroalgal phase shifts or reef resilience: links with diversity and functional roles of herbivorous fishes on the Great Barrier Reef. Coral Reefs. 2010;**29**(4):1005-1015

[132] Hughes TP, Graham NA, Jackson JB, Mumby PJ, Steneck RS. Rising to the challenge of sustaining coral reef resilience. Trends Ecol Evol. 2010;**25**(11):633-642

[133] Huang D. Threatened reef corals of the world. PLoS One. 2012;**7**(3):e34459