Chapter

Nutrition of Corals and Their Trophic Plasticity under Future Environmental Conditions

Walter Dellisanti, Davide Seveso and James Kar-Hei Fang

Abstract

Scleractinian corals obtain metabolic energy from their endosymbiotic autotrophic microalgae, and from remineralization of organic matter by bacteria and viruses, along with the heterotrophic food sources. The mutualistic symbiosis is generally stable but can be disrupted when environmental conditions surrounding the corals, such as increasing seawater temperature, become unfavorable to sustain each component of the holobiont. In this connection, the effects of global stressors such as climate change, and local stressors such as pollution, and their combination, are posing serious threats to the metabolic resistance of corals. However, some more resilient coral species have developed specific mechanisms to cope with fluctuating environmental conditions according to the trophic strategy (autotrophy, heterotrophy, or mixotrophy), and by modulating their energy expenditure. In this chapter, the role of nutrition in the coral symbiosis as the energetic budget for metabolic performance will be discussed, with a focus on the role of acquisition of nutrients through feeding, regulation of energy reserves (lipids, proteins, and carbohydrates), and adaptation capability in the natural environment, including the expression of heat-shock proteins (Hsps). Future environmental conditions under a combination of global changes and local impacts will also be discussed, with the aim of identifying the trophic niches of corals and geographical areas as possible refugia.

Keywords: energy, metabolism, adaptation, resistance, climate change

1. Introduction

Scleractinian corals are complex key habitat-forming organisms that create biogenic reef structures from shallow to deep waters [1], and they are fundamental to the supporting of the biodiversity of the world's oceans. They have evolved to thrive in conditions of optimal nutrient availability [2], seawater temperature, and oxygenation [3], and are in competition for space with other benthic taxa [4]. Mostly distributed along the tropics, corals can be found also in high-latitude subtropical areas and deep seas [5–8], where they show adaptive capability to live in fluctuating environmental conditions [9]. Corals can develop several biological structures depending on their capacity to grow via vertical or horizontal extension (**Figure 1**). These biogenic habitats formed by coral reefs represent one of the worldwide hotspots of biodiversity
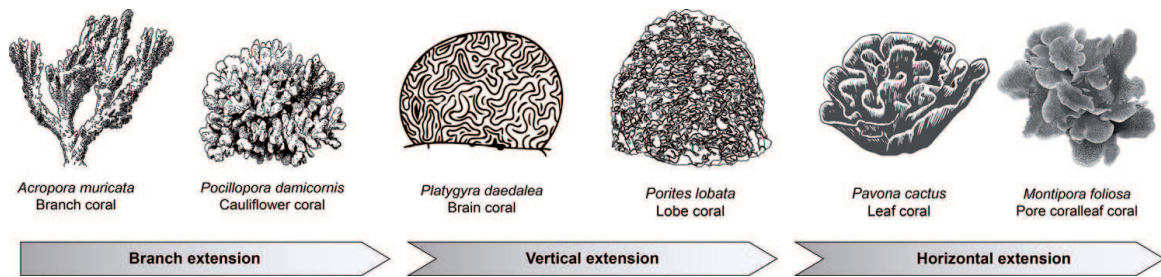
Figure 1.
Major scleractinian coral morphologies and different colony growth modes, based on branch, vertical, and horizontal extension. Modified from Pratchett et al. [10].

in the ocean [11], hosting a great variety of organisms, such as fish, macroalgae, and microorganisms [12].

Coral reefs can provide ecosystem goods and services, such as the provision of food, touristic activities, and protection of coastline from flooding and tidal movements [12, 13]. However, in the era of Anthropocene, coral reefs are among the habitats on Earth that are suffering the most and are dramatically degrading, since a multitude of factors are plaguing these marine ecosystems. Abiotic factors such as abnormally elevated or reduced temperatures, ocean acidification, high ultraviolet radiations, and fluctuation in salinity are increasing the occurrence of coral bleaching events [14–18]. Additionally, industrial pollution, coastal development, and excessive nutrient input, as well as biotic stressors such as predation outbreaks, epizootic diseases, and bioerosion are leading to further coral reef degradation around the world [19–22]. For all these reasons, corals are sensitive to changes in environmental conditions and therefore are considered good bioindicators of the health status of the marine environment [23, 24].

Corals are considered meta-organisms because of the complex biological interactions between the animal host and endosymbionts. Indeed, the concept of corals as holobiont encompasses the symbiotic relationship between dinoflagellate endosymbionts (Symbiodiniaceae [25]) and the animal host tissue (coral polyps), as well as the associated microorganisms found in coral tissue, gastric cavity, and coral skeleton. All components contribute to coral growth through the combined uptake of inorganic nutrients and food particles, photosynthesis, and deposition of calcium carbonate. In particular, the symbiotic relationship of corals is a mutual relationship between the coral polyps and the dinoflagellate endosymbionts. To gain metabolic energy, scleractinian corals are able to shift from heterotrophy (catching particulate food) [26, 27] to autotrophy (through photosynthesis by endosymbionts) [28]. Depending on the species-specific trophic strategy [29, 30], corals exhibit the ability to collect food particles (e.g. zooplankton) as a heterotrophic source of energy. On the other hand, they can rely on the autotrophic system of endosymbionts as an alternative source of oxygen and carbohydrates for aerobic respiration [31]. Oxygen availability determines the balance between the aerobic and anaerobic metabolic pathways, and therefore has significant implications for the energy budgets of corals [32]. These processes, however, are not perfectly balanced. Some species rely more on heterotrophy as an external source of energy, but some more on the photosynthetic system, while others are mixotrophic, meaning that they can increase the ability to modulate energy availability depending on the environmental conditions [30]. In all cases, the energy produced during the metabolic processes, which is stored as adenosine triphosphate (ATP), is used for maintaining the cellular physiology and supporting

the intracellular uptake of dissolved inorganic carbon to form calcium carbonate, which is necessary for building the skeleton and sustaining the growth of corals [33]. Energy reserves include proteins, lipids, and carbohydrates [27, 34] can be used when there is a high energy demand, e.g. under thermal stress [35].

Corals also harbor a large variety of microorganisms on their surface, which contribute to biogeochemical cycles and the provision of micronutrients. For instance, bacteria, archaea, and viruses play fundamental roles in the remineralization of organic matter into micronutrients [36]. The nutrition of corals is linked to the uptake of macro- and micronutrients that support the metabolic processes and growth [26]. The roles of micronutrients, such as nitrogen and iron, in enhancing the capacity of symbiosis have also been highlighted, in particular for the endosymbionts to resist abnormal conditions of surrounding waters [34]. The microorganisms living on the coral surface and in the tissue are also related to the probiotic diversity necessary for the general health of corals [37]. In case of disruption of the symbiotic equilibrium during extreme events (e.g. heatwaves or nutrient discharge) and prolonged disturbances (e.g. climate change or pollution), the microbial community can change from the symbiotic to commensal mode, a change that could reduce the capacity of the coral host to maintain the metabolic equilibrium [38].

In this context, the coral holobiont is capable of gaining metabolic energy from multiple sources and therefore has the capacity to modulate its physiology depending on nutrient availability and environmental conditions. The continuous pressures from anthropogenic activities are leading to substantial changes in the capability of corals to develop resistance mechanisms, which in turn define the characterization of coral species living in their specific environments. For instance, ocean warming and acidification are causing drastic changes that affect the sustainability of coral reef ecosystems, including food availability and services provided for humans [15, 39].

In this chapter, the nutrition in corals including recent advancements in the definition of coral health, energy budget, and performance under current environmental challenges of climate changes is explained, and the implications on the survival of corals are highlighted with the aim to define future reef habitats as refugia.

2. Coral nutrition

Corals are unique organisms capable of taking in nutrients and gaining energy for their metabolic processes, acting like nearly every trophic level in the marine ecosystem. For instance, it has been demonstrated that corals can behave simultaneously as: *i)* primary producer, by fixing carbon and producing biomass through photosynthesis; *ii)* primary consumer, by utilizing the products of photosynthesis; and *iii)* secondary and tertiary consumers, by degrading the substrate or taking in dissolved organic matter through the ingestion of zooplankton and bacteria [40]. Therefore, corals can optimize the feeding modes to contribute to the total daily energy budget according to the surrounding conditions. However, these processes depend mostly on light and food availability, and this determines the trophic niches and the metabolic plasticity to environmental changes [27].

2.1 Trophic niches

The diet of corals, however, goes beyond a fixed trophic strategy based on the morphology of polyps and corallites [41]. There is a need to consider trophic plasticity

as a critical factor of resistance to environmental stress [42]. The position of corals within the reef food web could be considered as the "*movement or storage of energy or materials*" [43] to identify the ecological functions of corals within such ecosystems. For example, energy allocation can shift from growth and reproduction under optimal environmental conditions to prioritizing long-term survival by depleting energy reserves under stress and shifting to anaerobic respiration of the coral hosts [44]. This concept has been applied to aquatic invertebrates, including corals, and the investigation of energy reserves based on the trophic strategy of corals is important to understand their metabolic responses to climate change, with significant implications on future coral refugia. Recently, scientific techniques have been advanced to define the trophic position of corals, and their plasticity within the reef niches. In this sense, the analysis of stable isotopes of carbon (δ^{13}C) and nitrogen (δ^{15}N) in coral samples allows the identification of either heterotrophic, autotrophic, or mixotrophic corals based on nutritional fluxes between coral hosts and endosymbionts [30, 45]. In this way, it is possible to recognize changes in trophic strategy (i.e. trophic plasticity) among different coral species living under the same environmental conditions [41]. This is particularly important in the ecological success of corals living in subtropical areas (**Figure 2**) [23] due to their capacity of using different nutrient sources to gain metabolic energy. Although the heterotrophic strategy has been suggested as a trophic key to enhancing bleaching resistance [45], the identification of the Symbiodiniaceae endosymbiont species and their role in acquiring essential nutrients needs to be considered as a thermotolerance feature of future corals [34].

2.2 Coral feeding

A substantial amount of energy in scleractinian corals is acquired through heterotrophy, which has become a key process to determine the resistance of corals to adverse conditions. Through heterotrophy, more energy for metabolic needs is available and therefore enhances the capability to resist stress events, which promotes bleaching resilience, raises protein levels, and in turn, supports the endosymbionts' physiological status [46]. Trophic differences are recognizable in the feeding rates of different species of corals. *Pocillopora* spp., for instance, have a higher capability to capture *Artemia* nauplii than *Acropora* spp. with different morphology, polyp extension, and feeding capacity. This, in turn, increases the growth rates and photosynthetic efficiency of endosymbionts, enhances the resistance to bleaching, and improves the general health status of corals [46, 47]. The key role of feeding is therefore not only related to increasing energy of the hosts but also supporting the processes involved in the endosymbionts, including photosynthesis and remineralization of organic matter. The transfer of nutrients between the hosts and endosymbionts has been recognized as inclusive of the mutualistic symbiosis of corals [48, 49]. The active intake of external organic matter, indeed, drives the acquisition of nitrogen fundamental for supporting the symbiont diversity and chlorophyll concentrations, conditions that are favorable to boost tissue growth, productivity, and calcification rates [50, 51]. Heterotrophy, however, is dependent on light, turbidity, and temperature, and can contribute to up to 35% of the metabolic energy in healthy corals [49] through assimilation of essential organic compounds of energy reserves such as lipids, proteins, and carbohydrates that cannot be acquired by photosynthesis only [46]. These are important biomarkers of coral physiology under climatic stress.
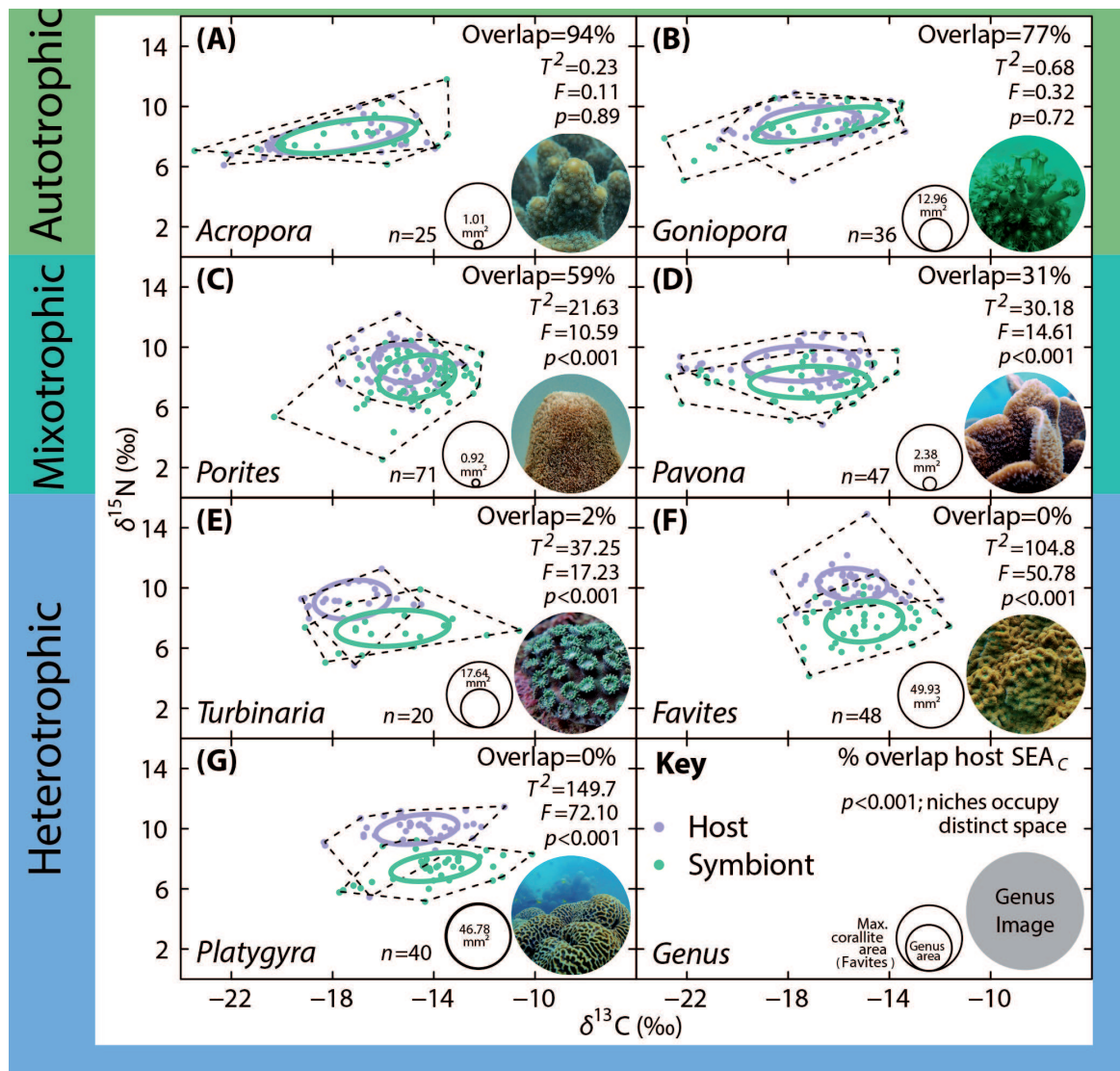
Figure 2.
Trophic niches of the coral hosts (purple) and photosynthetic endosymbionts (green) analyzed with the stable isotope Bayesian analysis (SIBER). The overlapping of $\delta^{13}C$ and $\delta^{15}N$ indicates different trophic strategies between autotrophy, mixotrophy, and heterotrophy. From Conti-Jerpe et al. [30]. Reprinted with permission from AAAS.

2.3 Energy reserves

Lipids are a fundamental component for the metabolic needs of corals and account for at least 30% of the energy reserves in corals [52]. These molecules indeed constitute much of the coral body composition, cells, and subcellular organelles [53]. The composition of fatty acids is mostly species-specific, and they are used as a chemotaxonomic indicator of the metabolic status of corals, and to trace the nutritional input of corals [54]. Polyunsaturated fatty acids (PUFAs) are one of the major lipids, and they are widely used as an indicator of dietary sources in heterotrophic corals for coping with metabolic stress [55]. It has been reported that when corals are exposed to high irradiance or heat stress, the intracellular PUFA content could decrease by up to 75% [56]. PUFAs are transported into coral compartments through feeding of zooplankton [57], and they reach the tissue after 1–2 weeks of incorporation [47]. The photosynthetic product supplied by endosymbionts is a second source

of PUFAs [46]. Moreover, the PUFA content can vary depending on the depth, season, and niche distribution of zooplankton in reef ecosystems [58] and in temperate waters [59].

Proteins are another key component of the coral cellular physiology, since they are involved in enzymatic catalysis, cellular transportation, immunity, and growth. Heterotrophic corals are able to have higher growth rates with higher tissue protein and lipid contents, which in turn facilitate calcification, tissue synthesis, and the formation of more polyps. Interestingly, recent studies have shown that scleractinian corals are not uniform in their morphology, and different parts of corals (core, branches, etc.) in different regions are functionally specialized to meet the specific energetic demands from coral surfaces to branches [60]. The field of proteomics, i.e. identification and quantification of cellular proteins, has been recently advancing with the aim to identify key physiological processes for uncovering cellular responses under environmental changes [61]. The expression of cellular stress molecular biomarkers represents a useful diagnostic tool to analyze changes in the cellular structural integrity and in the functional cellular pathways [62]. For instance, changes in the expression of heat-shock proteins (Hsps) are emerging as ubiquitous and putative markers of stress in corals [63–67]. Hsps are molecular chaperones that have vital cellular homeostatic and cytoprotective functions and represent one of the most important defense mechanisms of all organisms [68]. Hsps are present in different cellular compartments where they participate in various housekeeping tasks, such as proper protein folding, translocation of proteins between cellular compartments, and assembly of protein complexes [69, 70]. Hsps are classified by molecular weight in major chaperone families (Hsp40, Hsp60, Hsp70, Hsp90, Hsp100, and the small Hsps), which include several members with specific intracellular localization and functions [71].

Carbohydrates form an important component of the coral energy reserves because they are involved in the production of energetic metabolites such as ATP [72]. The production of ATP is crucial in all functions of the coral physiology, including cellular productivity, functioning, growth, and reproduction [44]. Carbohydrates in corals are acquired by both active capturing of food through heterotrophy and by translocation from the photosynthetic process. Excess carbohydrates can be released externally as a mucoid matrix [73, 74] or stored in tissue as lipids [75]. The coral mucus, a mucoid polysaccharide external layer, plays multiple roles. It serves as an attracting layer to capture food, a food source for bacteria by trapping organic particles [76, 77], and it also creates a probiotic pool to protect the holobiont from external pathogens and viruses [37, 78, 79].

For these reasons, carbohydrates are also considered an indicator of the coral health status. Indeed, the levels of intracellular carbohydrates indicate the capacity of corals to modulate thermal stress, and therefore indicate the thermotolerance of corals [35]. These findings suggest that elevated levels of carbohydrates are related to higher adaptation to future climatic conditions and reduced bleaching susceptibility to extreme events [80, 81].

3. Responses of corals to environmental changes

The coral holobiont is capable of modulating its metabolic processes to dissipate or gain energy from different sources depending on nutrient availability. However,

corals need to adopt special measures to face climatic change which is modifying the physicochemical and nutrient environment.

Anthropogenic activities are increasing levels of carbon dioxide (CO_2) in the atmosphere, leading to global warming and more frequent heatwaves, which are apparently associated with reduced rates of growth, calcification, and other functional traits, such as skeletal density, volume, and size[82–84]. These changes may in turn induce coral bleaching and mass mortality, and in the longer term, decline in coral biodiversity [81]. About a quarter of the atmospheric CO_2 dissolves in the ocean and reduces the seawater pH and carbonate saturation state, a process which is commonly known as ocean acidification. Ocean surface pH is expected to decrease by 0.3 units by 2100 under the RCP8.5 scenario [85, 86]. This, accompanied by cellular oxidative stress, can reduce the capacity of scleractinian corals and other calcifying organisms to build their calcium carbonate skeletons [87]. Besides global changes, human activities are responsible for multiple local pressures on marine ecosystems, specifically on corals. Coastal water quality declines in overpopulated areas, where high levels of dissolved inorganic nutrients cause eutrophication, sedimentation, and turbidity events [88–90]. The alteration of water conditions in the surface layer results in changes in the nutrient equilibrium (e.g. in the Redfield stoichiometry of C:N:P elements), which have brought about imbalanced physiological status of corals and their symbionts, and consequently increased frequency and severity of mass coral bleaching events [91, 92].

3.1 Responses to thermal stress

Among the plethora of stress factors, the rising of sea surface temperature due to global warming is certainly recognized as the prominent cause of coral bleaching inducing mass coral mortality [93, 94]. However, variable spatial and temporal patterns of mass bleaching have been extensively observed and can be generated by several factors that, by operating in combination, can determine different sensitivities of coral taxa to stressors [93, 95, 96]. For example, the extent of bleaching can depend on the duration and frequency of thermal anomalies and on-site-specific environmental conditions [97–100]. Nevertheless, several studies have pointed out that intrinsic factors of corals, including their morphological and physiological characteristics, play a fundamental role in determining the different levels of physiological resistance to environmental stress. In this context, the identity and clade of the Symbiodiniaceae partner may affect the coral susceptibility to unfavorable conditions [101–102].

Attempts to understand the differences in the response of corals to stress have also focused on coral physical properties, such as the coral morphology and tissue thickness, which influence growth, metabolic rates, and metabolite exchange across boundary layers and host CO_2 supply strategies [103, 104]. Therefore, faster growing branching taxa with thinner tissues appear more susceptible to elevated temperature than slower growing massive taxa with thicker tissues due to the latter's lower photoprotective capacity and ability to remove oxygen radicals generated during metabolic stress [103, 105].

3.2 Cellular stress responses

The cellular stress responses of corals are involved in driving spatial and temporal patterns of coral bleaching at both intra- and inter-specific levels. As sessile

organisms, corals cannot easily migrate to new environmental optima. Therefore, in order to cope with perturbations, they rely mainly on the efficiency of their molecular and cellular mechanisms, which represent the first line of defense in reducing the harmful effects of unfavorable conditions [106–108]. The capacity of acquiring metabolic energy from autotrophy rather than heterotrophy, and vice versa, is the key to a successful symbiotic relationship in corals. However, decreased capacity to take in nutrient has been observed during thermal stress along with reduced levels of dissolved inorganic nutrients [109], impairing the assimilation of carbon and nitrogen from the hosts' heterotrophy, and inducing starvation and parasitism [38]. Recent studies have identified positive correlation between the trophic status of host and endosymbionts in *Stylophora* proving that increased photosynthetic performance is related to the amount of inorganic nutrients assimilated and translocated between hosts and symbionts, and indicating that functional heterotrophy requires essential nutrients acquired through photosynthesis [42]. On the other hand, when facing an elevated nutrient concentration, corals might exhibit thermotolerance by maintaining symbionts as an autotrophic nutrient supply for the entire holobiont [42, 109] which suggests that nitrogen enrichment might enhance the resilience of corals to thermal stress [108]. In contrast, excessive nutrients in seawater have been linked to anthropogenic activities along the coastline, such as sewage plants, dredging, and agricultural activities. These conditions are typical of rapid urbanization and industrialization and are becoming critical for biogenic habitats near urban areas [7, 23, 110, 111]. Therefore, it is critical to identify and understand the trophic plasticity of corals in relation to nutrient availability and environmental stressors.

At the cellular level, Hsps are expressed under normal physiological conditions for maintenance of normal protein folding, signal transduction, and/or normal development [112]. Moreover, their expression is upregulated as a consequence of exposure to conditions that perturb cellular protein structures [69]. The expression of Hsps, and in particular that of Hsp70 and Hsp60, has been extensively analyzed in corals subjected to extreme temperatures and bleaching conditions [113–118]. However, Hsp modulation has also been observed in corals exposed to elevated light intensity [119, 120], salinity change [121, 122], and xenobiotics/nutrient enrichments [62, 118, 123]. Recently, it has been observed that Hsps may also play a role in the immune system of corals in response to pathogen invasion [65, 124]. In most of these studies, higher Hsp levels in corals generally infer higher protection toward environmental stressors and bleaching. For instance, corals with different susceptibilities to bleaching differ in their Hsp expression levels, with the bleaching-tolerant corals exhibiting higher expression levels than the bleaching-susceptible ones [96, 119]. A recent field study showed that healthy coral colonies of *Goniopora lobata* Milne Edwards [125] and *Porites lobata* Dana [126] of the central Red Sea had higher Hsp70 and Hsp60 levels than their respective naturally bleached counterparts [66].

In addition, high Hsp levels also contribute to corals adaptation to extreme conditions, such as those characterizing the shallow lagoons of the Maldivian reefs. There, despite the remarkable daily fluctuations in temperature and light and the regular exposure to higher temperature/light regimes than surrounding waters, which can exceed their tolerance threshold and would ordinarily induce stress and bleaching, Hsp modulation seems to play a protective role to prevent the rupture of symbiosis of corals [120]. Likewise, the Hsp levels have been found to be significantly higher in bleaching-tolerant corals originating from highly variable environments compared to corals that live in more stable environments. On Ofu Island (American Samoa),

colonies of *Acropora hyacinthus* Dana [126] from adjacent tidal pools with high daily thermal fluctuations were found to be more thermotolerant and had constitutively higher levels of Hsp70 gene compared to bleaching-sensitive colonies from less thermally variable pools [127]. Similarly, corals from inshore reefs of Florida bay *Porites astreoides,* Lamarck [128] were subjected to temperature fluctuations and appeared to have higher levels of Hsp genes than the offshore corals [107]. During the bleaching event of 2016, the near-shore colonies in Mauritius did not bleach and had significantly higher relative levels of both Hsp70 and 60 genes and protein compared to bleached reef colonies, indicating that the modulation of these Hsps was involved in local acclimatization of corals to their environments [96]. However, it is important to consider that prior exposure to sublethal environment stress (preconditioning) that resulted in later tolerance to bleaching temperatures [129] and changes in the expression of specific genes, such as those of Hsps, have been associated with this thermal tolerance plasticity [130, 131]. For example, the preconditioning of *Acropora millepora* (Ehrenberg, 1834) colonies to heat stress accounted for increased gene expression and tolerance to bleaching compared to nonpreconditioned colonies [63]. Overall, the expression pattern of Hsps and the amplitude of their modulation may show species-specific characteristics, which may reflect different mechanisms and abilities of stress response.

3.3 Thermal performance

Metabolic performance, in particular the thermal performance curve (TPC) which defines the nonlinear relationship of organismal metabolism versus a given source of stress, is another parameter to consider when coral health is concerned. When the metabolic response of corals to low/high temperature is considered, the TPC can be applied to quantify the response of a coral species to thermal stress [132]. Moreover, through the TPC, it is possible to measure the maximum level of such performance, the optimal conditions of temperature, and the capacity of resistance to temperature variation (e.g. thermal breadth). The shape of such curve and its relative breadth will determine the metabolic plasticity of organisms (corals) to temperature variations. This can be used to define the physiological performance of corals and compare their specific responses in the subtropical area to indicate physiological adaptation of corals to living conditions and the challenges that subtropical corals face when optimizing their productivity in subtropical environments [133]. The heritability of coral traits must also be considered in the framework of coral adaptation to future conditions of climate change to better predict the evolution of corals in suboptimal conditions [134].

4. Future coral refugia

Coral reefs are often described as biogenic structures which provide nutriments and services to the marine ecosystems formed in oligotrophic areas (i.e. low dissolved nutrients and clear water) with stable environmental conditions. These features are usually optimal for bioconstruction, such as corals, to capture carbonates from seawater and sustain the metabolic energy needed for growth and reproduction [93, 135]. The capacity of corals to modulate their metabolism according to surrounding conditions is the key for their success. Scleractinian corals are thriving also in the

so-called marginal reefs, where thermal and salinity anomalies, eutrophication, and elevated sedimentation rates are the causes of metabolic expenditures and, eventually, stress [136–139].

Marginal reefs are located at high latitudes of subtropical areas and near mega-lopolis. Corals living in these areas receive multiple pressures from local stressors together with global changes, although the processes involved in these ecosystems operate at different spatial (i.e. geographical) and temporal (i.e. frequency of stress events) scales compared to tropical reefs. In this context, it is important to consider how natural evolution, affected by human pressures, has shaped the coral species living in these areas, and how the marginal reefs can act as refuge area for future conditions. Refugia are considered as those areas with the ability to provide protection from multiple stressors [140], and in this case coral refugia are identified as areas where long-term stressors are low that less likely to influence coral survival. For examples, considering the evolutionary timescales, the current marginal reefs are already serving as refugia due to their environmental conditions [9], although with reduced speciation, growth, and reproduction rates [141]. Moreover, most of the research works have focused on the short-term relief to environmental stressors, and there is a need to understand how the marginal reefs can act as refugia under the climatic scenarios of more frequent heatwave events and continuous development of coastal areas [142]. The understanding of the responses of corals in the adaptation and evolution in these areas is therefore a priority for devising conservation and restoration measures for the future coral reefs [3]. Recent studies have identified areas as future refugia from thermal stress. Corals living in environments with naturally high temperature fluctuation may have developed higher thermal tolerance to heat stress, and therefore these areas can be considered as refugia for future conditions. To represent refugia areas with a high potential to maintain the future coral biodiversity and ecosystem functions, the frequency of thermal stress events (e.g. 12-week sum of 1°C higher than the maximum monthly mean) should be less than one every 10 years [143]. Future warming conditions and more heatwaves might result in too frequent thermal stress events and leave no room for those corals and other marine organisms that live in thermal refugia to adapt. The biological responses to the chronic development of ocean warming will be critical to determine the effectiveness of high-latitude reefs as the thermal refugia [143].

5. Conclusion

Coral reefs have very high biodiversity values and provide important ecosystem services, with the capacity to resist anthropogenic stress by modulating their energetic budgets as described in this chapter. Current major threats to them are caused by increasing seawater temperature (ocean warming) and reduced pH level (ocean acidification), which cause reduction in survival, calcification, growth, and photosynthesis in several marine taxa [138, 144] with the levels of impacts depending on morphology and the feeding capacity of corals [45]. There are global consequences of this reduced capacity of reef ecosystems to provide crucial services, such as reduced fishing capacity and unsustainable management of marine reserves [145, 146]. A deep understanding of the multiple interactions between stressors and mitigators will be crucial to define the trophic plasticity and reef responses under the future environmental changes.

Acknowledgements

Conflict of interest

The authors declare no conflict of interest.

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References

[1] Buhl-Mortensen L, Vanreusel A, Gooday AJ, et al. Biological structures as a source of habitat heterogeneity and biodiversity on the deep ocean margins. Marine Ecology. 2010;**31**(1):21-50. DOI: 10.1111/J.1439-0485.2010.00359.X

[2] Enochs IC, Manzello DP, Donham EM, et al. Shift from coral to macroalgae dominance on a volcanically acidified reef. Nature Climate Change. 2015;**5**(12):1083-1088. DOI: 10.1038/nclimate2758

[3] Camp EF, Schoepf V, Mumby PJ, et al. The future of coral reefs subject to rapid climate change: Lessons from natural extreme environments. Frontiers in Marine Science. 2018;**5**:1-21. DOI: 10.3389/fmars.2018.00004

[4] López-Victoria M, Zea S, Weil E. Competition for space between encrusting excavating Caribbean sponges and other coral reef organisms. Marine Ecology Progress Series. 2006;**312**:113-121. DOI: 10.3354/MEPS312113

[5] Chui APY, Yeung CW, Tsang RHL, et al. Lowered temperature and reduced salinity retarded development of early life history stages of Acropora valida from the marginal environment. Regional Studies in Marine Science. 2016;**8**:430-438. DOI: 10.1016/j.rsma.2016.04.004

[6] Kurihara H, Wouters J, Yasuda N. Seasonal calcification of the coral Acropora digitifera from a subtropical marginal Okinawa reef under ocean acidification. Coral Reefs. 2019;**38**(3):443-454. DOI: 10.1007/s00338-019-01794-9

[7] Heery EC, Hoeksema BW, Browne NK, et al. Urban coral reefs: Degradation and resilience of hard coral assemblages in coastal cities of east and Southeast Asia. Marine Pollution Bulletin. 2018;**135**:654-681. DOI: 10.1016/j.marpolbul.2018.07.041

[8] Chimienti G, Mastrototaro F, D'Onghia G. Mesophotic and deep-sea vulnerable coral habitats of the Mediterranean Sea: Overview and conservation perspectives. In: Advances in the Studies of the Benthic Zone. Rijeka: IntechOpen; 2019. DOI: 10.5772/intechopen.90024

[9] Lybolt M, Neil D, Zhao J, Feng Y, Yu K-F, Pandolfi J. Instability in a marginal coral reef: The shift from natural variability to a human-dominated seascape. Frontiers in Ecology and the Environment. 2011;**9**(3):154-160. DOI: 10.1890/090176

[10] Pratchett MS, Anderson KD, Hoogenboom MO, Widman E, Baird AH, Pandolfi JM, et al. Spatial, temporal and taxonomic variation in coral growth - implications for the structure and function of coral reef ecosystems. Oceanography and Marine Biology: An Annual Review. 2015;**53**:215-295

[11] Roberts CM, McClean CJ, Veron JEN, et al. Marine biodiversity hotspots and conservation priorities for tropical reefs. Science. 2002;**295**(5558):1280-1284. DOI: 10.1126/science.1067728

[12] Knowlton N, Brainard RE, Fisher R, Moews M, Plaisance L, Caley MJ. Coral reef biodiversity. In: McIntyre AD, editor. Life in the World's Oceans. Oxford, UK: Wiley-Blackwell; 2010. pp. 65-78. DOI: 10.1002/9781444325508.ch4

[13] Van Zanten BT, Van Beukering PJH, Wagtendonk AJ. Coastal protection

by coral reefs: A framework for spatial assessment and economic valuation. Ocean and Coastal Management. 2014;**96**:94-103. DOI: 10.1016/j. ocecoaman.2014.05.001

[14] Hoegh-Guldberg O, Mumby PJ, Hooten AJ, et al. Coral reefs under rapid climate change and ocean acidification. Science. 2007;**318**(5857):1737-1743. DOI: 10.1126/science.1152509

[15] Hughes TP, Barnes ML, Bellwood DR, et al. Coral reefs in the Anthropocene. Nature. 2017;**546**(7656):82-90. DOI: 10.1038/nature22901

[16] Moss RH, Edmonds JA, Hibbard KA, et al. The next generation of scenarios for climate change research and assessment. Nature. 2010;**463**(7282):747-756. DOI: 10.1038/nature08823

[17] Ellis JI, Jamil T, Anlauf H, et al. Multiple stressor effects on coral reef ecosystems. Global Change Biology. 2019;**25**(12):4131-4146. DOI: 10.1111/ GCB.14819

[18] Dellisanti W, Chung JTH, Chow CFY, Wu J, Wells ML, Chan LL. Experimental techniques to assess coral physiology in situ under global and local stressors: Current approaches and novel insights. Frontiers in Physiology. 2021;**12**:656562. DOI: 10.3389/fphys.2021.656562

[19] Nyström M, Folke C, Moberg F. Coral reef disturbance and resilience in a human-dominated environment. Trends in Ecology & Evolution. 2000;**15**(10):413-417. DOI: 10.1016/ S0169-5347(00)01948-0

[20] Szmant AM. Nutrient enrichment on coral reefs: Is it a major cause of coral reef decline? Estuaries. 2002;**25**(4):743-766. DOI: 10.1007/BF02804903

[21] Fabricius KE, De'ath, G. Identifying ecological change and its cause: A

case study on coral reefs. Ecological Applications. 2004;**14**(5):1448-1465. DOI: 10.1890/03-5320

[22] Bruno JF, Selig ER, Casey KS, et al. Thermal stress and coral cover as drivers of coral disease outbreaks. PLoS Biology. 2007;**5**(6):e124. DOI: 10.1371/JOURNAL. PBIO.0050124

[23] Lachs L, Johari NAM, Le DQ, et al. Effects of tourism-derived sewage on coral reefs: Isotopic assessments identify effective bioindicators. Marine Pollution Bulletin. 2019;**148**:85-96. DOI: 10.1016/J. MARPOLBUL.2019.07.059

[24] Metian M, Hédouin L, Ferrier-Pagès C, et al. Metal bioconcentration in the scleractinian coral Stylophora pistillata: Investigating the role of different components of the holobiont using radiotracers. Environmental Monitoring and Assessment. 2015;**187**(4):1-10. DOI: 10.1007/ s10661-015-4383-z

[25] LaJeunesse TC, Parkinson JE, Gabrielson PW, et al. Systematic revision of Symbiodiniaceae highlights the antiquity and diversity of coral endosymbionts. Current Biology. 2018;**28**(16):2570-2580. DOI: 10.1016/j. cub.2018.07.008

[26] Fox MD, Elliott Smith EA, Smith JE, Newsome SD. Trophic plasticity in a common reef-building coral: Insights from δ13C analysis of essential amino acids. Functional Ecology. 2019;**33**(11):2203-2214. DOI: 10.1111/1365-2435.13441

[27] Grottoli AG, Tchernov D, Winters G. Physiological and biogeochemical responses of super-corals to thermal stress from the northern Gulf of Aqaba, Red Sea. Frontiers in Marine Science. 2017;**4**:215. DOI: 10.3389/ fmars.2017.00215

[28] Wangpraseurt D, Pernice M, Guagliardo P, et al. Light microenvironment and single-cell gradients of carbon fixation in tissues of symbiont-bearing corals. The ISME Journal. 2015;**10**(3):788-792. DOI: 10.1038/ismej.2015.133

[29] Carbonne C, Teixidó N, Moore B, et al. Two temperate corals are tolerant to low pH regardless of previous exposure to natural CO_2 vents. Limnology and Oceanography. 2021;**66**(11):4046-4061. DOI: 10.1002/LNO.11942

[30] Conti-Jerpe IE, Thompson PD, Wong CWM, et al. Trophic strategy and bleaching resistance in reef-building corals. Science Advances. 2020;**6**(15):5443-5453. DOI: 10.1126/sciadv.aaz5443

[31] Gardella DJ, Edmunds PJ. The oxygen microenvironment adjacent to the tissue of the scleractinian Dichocoenia stokesii and its effects on symbiont metabolism. Marine Biology. 1999;**135**(2):289-295. DOI: 10.1007/s002270050626

[32] Linsmayer LB, Deheyn DD, Tomanek L, Tresguerres M. Dynamic regulation of coral energy metabolism throughout the diel cycle. Scientific Reports. 2020;**10**(1):1-11. DOI: 10.1038/s41598-020-76828-2

[33] Comeau S, Tambutté E, Carpenter RC, et al. Coral calcifying fluid pH is modulated by seawater carbonate chemistry not solely seawater pH. Proceedings of the Royal Society B: Biological Sciences. 1847;**2017**:284. DOI: 10.1098/rspb.2016.1669

[34] Reich HG, Tu WC, Rodriguez IB, et al. Iron availability modulates the response of Endosymbiotic dinoflagellates to heat stress. Journal of Phycology. 2021;**57**(1):3-13. DOI: 10.1111/JPY.13078

[35] Kochman NR, Grover R, Rottier C, Ferrier-Pages C, Fine M. The reef building coral Stylophora pistillata uses stored carbohydrates to maintain ATP levels under thermal stress. Coral Reefs. 2021;**40**(5):1473-1485. DOI: 10.1007/S00338-021-02174-Y/FIGURES/4

[36] Thurber RLV, Correa AMS. Viruses of reef-building scleractinian corals. Journal of Experimental Marine Biology and Ecology. 2011;**408**(1-2):102-113. DOI: 10.1016/j.jembe.2011.07.030

[37] Peixoto RS, Rosado PM, de Assis Leite DC, Rosado AS, Bourne DG. Beneficial microorganisms for corals (BMC): Proposed mechanisms for coral health and resilience. Frontiers in Microbiology. 2017;**8**:1-16. DOI: 10.3389/fmicb.2017.00341

[38] Baker DM, Freeman CJ, Wong JCYY, Fogel ML, Knowlton N. Climate change promotes parasitism in a coral symbiosis. The ISME Journal. 2018;**12**(3):921-930. DOI: 10.1038/s41396-018-0046-8

[39] Putnam HM, Barott KL, Ainsworth TD, Gates RD. The vulnerability and resilience of reef-building corals. Current Biology. 2017;**27**(11):R528-R540. DOI: 10.1016/j.cub.2017.04.047

[40] Muscatine L, Porter JW. Reef corals: Mutualistic symbioses adapted to nutrient-poor environments. Bioscience. 1977;**27**(7):454-460. DOI: 10.2307/1297526

[41] Sturaro N, Hsieh YE, Chen Q, Wang PL, Denis V. Trophic plasticity of mixotrophic corals under contrasting environments. Functional Ecology. 2021;**35**(12):2841-2855. DOI: 10.1111/1365-2435.13924/SUPPINFO

[42] Ezzat L, Maguer JF, Grover R, Rottier C, Tremblay P, Ferrier-Pagès C.

Nutrient starvation impairs the trophic plasticity of reef-building corals under ocean warming. Functional Ecology. 2019;**33**(4):643-653. DOI: 10.1111/1365-2435.13285/SUPPINFO

[43] Bellwood DR, Streit RP, Brandl SJ, Tebbett SB. The meaning of the term 'function' in ecology: A coral reef perspective. Functional Ecology. 2019;**33**(6):948-961. DOI: 10.1111/1365-2435.13265/SUPPINFO

[44] Sokolova IM, Frederich M, Bagwe R, Lannig G, Sukhotin AA. Energy homeostasis as an integrative tool for assessing limits of environmental stress tolerance in aquatic invertebrates. Marine Environmental Research. 2012;**79**:1-15. DOI: 10.1016/J. MARENVRES.2012.04.003

[45] Ferrier-Pagès C, Sauzéat L, Balter V. Coral bleaching is linked to the capacity of the animal host to supply essential metals to the symbionts. Global Change Biology. 2018;**24**(7):3145-3157. DOI: 10.1111/GCB.14141

[46] Huang YL, Mayfield AB, Fan TY. Effects of feeding on the physiological performance of the stony coral Pocillopora acuta. Scientific Reports. 2020;**10**(1):1-12. DOI: 10.1038/s41598-020-76451-1

[47] Lim CS, Bachok Z, Hii YS. Effects of supplementary polyunsaturated fatty acids on the health of the scleractinian coral Galaxea fascicularis (Linnaeus, 1767). Journal of Experimental Marine Biology and Ecology. 2017;**491**:1-8. DOI: 10.1016/j.jembe.2017.02.009

[48] Anthony KRN, Fabricius KE. Shifting roles of heterotrophy and autotrophy in coral energetics under varying turbidity. Journal of Experimental Marine Biology and

Ecology. 2000;**252**(2):221-253. DOI: 10.1016/S0022-0981(00)00237-9

[49] Houlbrèque F, Ferrier-Pagès C. Heterotrophy in tropical Scleractinian corals. Biological Reviews. 2009;**84**(1):1-17. DOI: 10.1111/J.1469-185X.2008.00058.X

[50] Ferrier-Pagès C, Witting J, Tambutté E, Sebens KP. Effect of natural zooplankton feeding on the tissue and skeletal growth of the scleractinian coral Stylophora pistillata. Coral Reefs. 2003;**22**(3):229-240. DOI: 10.1007/S00338-003-0312-7/TABLES/3

[51] Yu X, Jiang L, Gan J, et al. Effects of feeding on production, body composition and fatty acid profile of scleractinian coral Galaxea fascicularis. Aquaculture Reports. 2021;**21**:100871. DOI: 10.1016/J. AQREP.2021.100871

[52] Parrish CC. Lipids in marine ecosystems. ISRN Oceanography. 2013;**2013**:1-16. DOI: 10.5402/2013/604045

[53] Liu CY, Zhang F, Sun YF, Yu XL, Huang H. Effects of nitrate enrichment on respiration, photosynthesis, and fatty acid composition of reef coral *Pocillopora damicornis* larvae. Frontiers in Marine Science. 2020;7:531. DOI: 10.3389/FMARS.2020.00531/BIBTEX

[54] Mies M, Güth AZ, Tenório AA, et al. In situ shifts of predominance between autotrophic and heterotrophic feeding in the reef-building coral Mussismilia hispida: An approach using fatty acid trophic markers. Coral Reefs. 2018;**37**(3):677-689. DOI: 10.1007/S00338-018-1692-Z/FIGURES/7

[55] Seemann J, Sawall Y, Auel H, Richter C. The use of lipids and fatty acids to measure the trophic plasticity of the coral Stylophora subseriata. Lipids.

2013;**48**(3):275-286. DOI: 10.1007/ S11745-012-3747-1

[56] Bachok Z, Mfilinge P, Tsuchiya M. Characterization of fatty acid composition in healthy and bleached corals from Okinawa, Japan. Coral Reefs. 2006;**25**(4):545-554. DOI: 10.1007/ S00338-006-0130-9/TABLES/3

[57] Tagliafico A, Rudd D, Rangel MS, et al. Lipid-enriched diets reduce the impacts of thermal stress in corals. Marine Ecology Progress Series. 2017;**573**:129-141. DOI: 10.3354/MEPS12177

[58] Latyshev NA, Naumenko NV, Svetashev VI, Latypov YY. Fatty acids of reef-building corals. Marine Ecology Progress Series. 1991;**76**:295-301

[59] Rodolfo-Metalpa R, Peirano A, Houlbrèque F, Abbate M, Ferrier-Pagès C. Effects of temperature, light and heterotrophy on the growth rate and budding of the temperate coral Cladocora caespitosa. Coral Reefs. 2008;**27**(1):17-25. DOI: 10.1007/ S00338-007-0283-1/FIGURES/5

[60] Conlan JA, Humphrey CA, Severati A, Francis DS. Intra-colonial diversity in the scleractinian coral, *Acropora millepora* : Identifying the nutritional gradients underlying physiological integration and compartmentalised functioning. PeerJ. 2018;**6**:e4239. DOI: 10.7717/peerj.4239

[61] Ma H, Liao H, Dellisanti W, Sun Y, Chan LL, Zhang L. Characterizing the host coral proteome of Platygyra carnosa using suspension trapping (S-trap). Journal of Proteome Research. 2021;**20**(3):1783-1791. DOI: 10.1021/ACS. JPROTEOME.0C00812

[62] Downs CA. Cellular diagnostics and its application to aquatic and marine toxicology. In: Ostrander GK, editor. Techniques in Aquatic Toxicology. Vol. 2. Boca Raton, USA: CRC Press; 2010

[63] Bellantuono AJ, Granados-Cifuentes C, Miller DJ, Hoegh-Guldberg O, Rodriguez-Lanetty M. Coral thermal tolerance: Tuning gene expression to resist thermal stress. PLoS One. 2012;**7**(11):50685. DOI: 10.1371/ JOURNAL.PONE.0050685

[64] Louis YD, Bhagooli R, Kenkel CD, Baker AC, Dyall SD. Gene expression biomarkers of heat stress in scleractinian corals: Promises and limitations. Comparative Biochemistry and Physiology, Part C: Toxicology & Pharmacology. 2017;**191**:63-77. DOI: 10.1016/J.CBPC.2016.08.007

[65] Seveso D, Montano S, Reggente MAL, et al. The cellular stress response of the scleractinian coral Goniopora columna during the progression of the black band disease. Cell Stress & Chaperones. 2017;**22**(2):225-236. DOI: 10.1007/ S12192-016-0756-7/FIGURES/1

[66] Seveso D, Arrigoni R, Montano S, et al. Investigating the heat shock protein response involved in coral bleaching across scleractinian species in the Central Red Sea. Coral Reefs. 2020;**39**(1):85-98. DOI: 10.1007/S00338-019-01878-6/FIGURES/1

[67] Traylor-Knowles N, Rose NH, Sheets EA, Palumbi SR. Early transcriptional responses during heat stress in the coral Acropora hyacinthus. The Biological Bulletin. 2017;**232**(2):91-100. DOI: 10.1086/692717/ASSET/ IMAGES/LARGE/FGA1.JPEG

[68] Kumsta C, Jakob U. Redox-regulated chaperones. Biochemistry. 2009;**48**(22):4666-4676. DOI: 10.1021/ BI9003556

[69] Balchin D, Hayer-Hartl M, Hartl FU. In vivo aspects of protein folding and quality

control. Science. 2016;**353**(6294):4354. DOI: 10.1126/science.aac4354

[70] Rosenzweig R, Nillegoda NB, Mayer MP, Bukau B. The Hsp70 chaperone network. Nature Reviews. Molecular Cell Biology. 2019;**20**(11):665-680. DOI: 10.1038/S41580-019-0133-3

[71] Pockley AG, Georgiades A, Thulin T, De Faire U, Frostegård J. Serum heat shock protein 70 levels predict the development of atherosclerosis in subjects with established hypertension. Hypertension. 2003;**42**(3):235-238. DOI: 10.1161/01.HYP.0000086522.13672.23

[72] Hardie DG, Scott JW, Pan DA, Hudson ER. Management of cellular energy by the AMP-activated protein kinase system. FEBS Letters. 2003;**546**(1):113-120. DOI: 10.1016/S0014-5793(03)00560-X

[73] Hadaidi G, Gegner HM, Ziegler M, Voolstra CR. Carbohydrate composition of mucus from scleractinian corals from the Central Red Sea. Coral Reefs. 2019;**38**(1):21-27. DOI: 10.1007/s00338-018-01758-5

[74] Wild C, Naumann M, Niggl W, Haas A. Carbohydrate composition of mucus released by scleractinian warm- and cold-water reef corals. Aquatic Biology. 2010;**10**(1):41-45. DOI: 10.3354/AB00269

[75] Patton JS, Burris JE. Lipid synthesis and extrusion by freshly isolated zooxanthellae (symbiotic algae). Marine Biology. 1983;**75**(2-3):131-136. DOI: 10.1007/BF00405995

[76] Hadaidi G, Röthig T, Yum LK, et al. Stable mucus-associated bacterial communities in bleached and healthy corals of Porites lobata from the Arabian seas. Scientific Reports. 2017;**7**:1-11. DOI: 10.1038/srep45362

[77] Wild C, Woyt H, Huettel M. Influence of coral mucus on nutrient fluxes in carbonate sands. Marine Ecology Progress Series. 2005;**287**:87-98. DOI: 10.3354/meps287087

[78] Sweet M, Bythell J. The role of viruses in coral health and disease. Journal of Invertebrate Pathology. 2017;**147**:136-144. DOI: 10.1016/j.jip.2016.12.005

[79] Glasl B, Herndl GJ, Frade PR. The microbiome of coral surface mucus has a key role in mediating holobiont health and survival upon disturbance. The ISME Journal. 2016;**10**(9):2280-2292. DOI: 10.1038/ismej.2016.9

[80] Hoegh-Guldberg O, Mumby PJ, Hooten AJ, et al. Coral reefs under rapid climate change and ocean acidification. Science. 2007;**318**(5857):1737-1742. DOI: 10.1126/science.1152509

[81] Hughes TP, Kerry JT, Álvarez-Noriega M, et al. Global warming and recurrent mass bleaching of corals. Nature. 2017;**543**(7645):373-377. DOI: 10.1038/nature21707

[82] Schoepf V, D'Olivo JP, Rigal C, Jung EMU, McCulloch MT. Heat stress differentially impacts key calcification mechanisms in reef-building corals. Coral Reefs. 2021;**40**(2):459-471. DOI: 10.1007/s00338-020-02038-x

[83] Gruber N, Boyd PW, Frölicher TL, Vogt M. Biogeochemical extremes and compound events in the ocean. Nature. 2021;**600**(7889):395-407. DOI: 10.1038/s41586-021-03981-7

[84] Donovan MK, Burkepile DE, Kratochwill C, et al. Local conditions magnify coral loss after marine heatwaves. Science. 2021;**372**(6545):977-980. DOI: 10.1126/science.abd9464

[85] Ciais P, Sabine C, Bala G, Peters W. Carbon and other biogeochemical cycles. In: Stocker et al., editors. Climate Change 2013 the Physical Science Basis: Working Group I Contribution to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change; United Kingdom, New York, USA: Cambridge University Press; 2013. pp. 465-570. DOI: 10.1017/CBO9781107415324.015

[86] Zeebe RE, Wolf-Gladrow D, Zakaria FZ, et al. Effects of ocean acidification on benthic processes, organisms, and ecosystems. In: Chen CA, editor. Climate Change 2013 the Physical Science Basis: Working Group I Contribution to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change; United Kingdom, New York, USA: Cambridge University Press; 2013. pp. 122-153. DOI: 10.1017/CBO9781107415324.015

[87] Eyre BD, Andersson AJ, Cyronak T. Benthic coral reef calcium carbonate dissolution in an acidifying ocean. Nature Climate Change. 2014;**4**(11):969-976. DOI: 10.1038/nclimate2380

[88] Burkepile DE, Shantz AA, Adam TC, et al. Nitrogen identity drives differential impacts of nutrients on coral bleaching and mortality. Ecosystems. 2020;**23**(4):798-811. DOI: 10.1007/s10021-019-00433-2

[89] Browne NK, Precht E, Last KS, Todd PA. Photo-physiological costs associated with acute sediment stress events in three near-shore turbid water corals. Marine Ecology Progress Series. 2014;**502**(April):129-143. DOI: 10.3354/meps10714

[90] Tuttle LJ, Johnson C, Kolinski S, Minton D, Donahue MJ. How does sediment exposure affect corals? A systematic review protocol.

Environmental Evidence. 2020;**9**(1):17. DOI: 10.1186/s13750-020-00200-0

[91] D'Angelo C, Wiedenmann J. Impacts of nutrient enrichment on coral reefs: New perspectives and implications for coastal management and reef survival. Current Opinion in Environment Sustainability. 2014;7:82-93. DOI: 10.1016/j.cosust.2013.11.029

[92] Morris LA, Voolstra CR, Quigley KM, Bourne DG, Bay LK. Nutrient availability and metabolism affect the stability of coral–Symbiodiniaceae symbioses. Trends in Microbiology. 2019;**27**(8):678-689. DOI: 10.1016/j.tim.2019.03.004

[93] Hughes TP, Anderson KD, Connolly SR, et al. Spatial and temporal patterns of mass bleaching of corals in the Anthropocene. Science. 2018;**359**(6371):80-83. DOI: 10.1126/science.aan8048

[94] Sully S, Burkepile DE, Donovan MK, Hodgson G, van Woesik R. A global analysis of coral bleaching over the past two decades. Nature Communications. 2019;**10**(1):1-5. DOI: 10.1038/s41467-019-09238-2

[95] Heron SF, Maynard JA, Van Hooidonk R, Eakin CM. Warming trends and bleaching stress of the World's coral reefs 1985-2012. Scientific Reports. 2016;**6**(1):1-14. DOI: 10.1038/srep38402

[96] Louis YD, Bhagooli R, Seveso D, et al. Local acclimatisation-driven differential gene and protein expression patterns of Hsp70 in Acropora muricata: Implications for coral tolerance to bleaching. Molecular Ecology. 2020;**29**(22):4382-4394. DOI: 10.1111/MEC.15642

[97] McClanahan TR, Maina J. Response of coral assemblages to the interaction between natural temperature variation

and rare warm-water events. Ecosystems. 2003;**6**(6):551-563. DOI: 10.1007/S10021-002-0104-X/TABLES/3

[98] Guest JR, Baird AH, Maynard JA, et al. Contrasting patterns of coral bleaching susceptibility in 2010 suggest an adaptive response to thermal stress. PLoS One. 2012;**7**(3):e33353. DOI: 10.1371/JOURNAL.PONE.0033353

[99] Howells EJ, Berkelmans R, Van Oppen MJH, Willis BL, Bay LK. Historical thermal regimes define limits to coral acclimatization. Ecology. 2013;**94**(5):1078-1088. DOI: 10.1890/12-1257.1

[100] Pratchett MS, McCowan D, Maynard JA, Heron SF. Changes in bleaching susceptibility among corals subject to ocean warming and recurrent bleaching in Moorea, French Polynesia. PLoS One. 2013;**8**(7):e70443. DOI: 10.1371/JOURNAL.PONE.0070443

[101] Hume BCC, Voolstra CR, Arif C, et al. Ancestral genetic diversity associated with the rapid spread of stress-tolerant coral symbionts in response to holocene climate change. Proceedings of the National Academy of Sciences of the United States of America. 2016;**113**(16):4416-4421. DOI: 10.1073/pnas.1601910113

[102] Ziegler M, Eguíluz VM, Duarte CM, Voolstra CR. Rare symbionts may contribute to the resilience of coral–algal assemblages. The ISME Journal. 2017;**12**(1):161-172. DOI: 10.1038/ismej.2017.151

[103] Loya Y, Sakai K, Yamazato K, Nakano Y, Sambali H, Van Woesik R. Coral bleaching: The winners and the losers. Ecology Letters. 2001;**4**(2):122-131. DOI: 10.1046/j.1461-0248.2001.00203.x

[104] Darling ES, Alvarez-Filip L, Oliver TA, Mcclanahan TR, Côté IM. Evaluating life-history strategies of reef corals from species traits. Ecology Letters. 2012;**15**(12):1378-1386. DOI: 10.1111/j.1461-0248.2012.01861.x

[105] Hoegh-Guldberg O. Climate change, coral bleaching and the future of the world's coral reefs. Marine and Freshwater Research. 1999;**50**(8):839-866. DOI: 10.1071/MF99078

[106] Brown BE. Coral bleaching: Causes and consequences. Coral Reefs. 1997;**16**(1):S129-S138. DOI: 10.1007/S003380050249

[107] Kenkel CD, Sheridan C, Leal MC, et al. Diagnostic gene expression biomarkers of coral thermal stress. Molecular Ecology Resources. 2014;**14**(4):667-678. DOI: 10.1111/1755-0998.12218

[108] Rosic N, Kaniewska P, Chan CKK, et al. Early transcriptional changes in the reef-building coral Acropora aspera in response to thermal and nutrient stress. BMC Genomics. 2014;**15**(1):1-17. DOI: 10.1186/1471-2164-15-1052/FIGURES/6

[109] Naugle MS, Oliver TA, Barshis DJ, Gates RD, Logan CA. Variation in coral Thermotolerance across a pollution gradient erodes as coral symbionts shift to more heat-tolerant genera. Frontiers in Marine Science. 2021;**8**:1670. DOI: 10.3389/FMARS.2021.760891/BIBTEX

[110] Duprey NN, Yasuhara M, Baker DM. Reefs of tomorrow: Eutrophication reduces coral biodiversity in an urbanized seascape. Global Change Biology. 2016;**22**(11):3550-3565. DOI: 10.1111/gcb.13432

[111] Duprey NN, Wang TX, Kim T, et al. Megacity development and the demise of coastal coral communities: Evidence

from coral skeleton δ ^{15} N records in the Pearl River estuary. Global Change Biology. 2020;**26**(3):1338-1353. DOI: 10.1111/gcb.14923

[112] Chen JY, Parekh M, Seliman H, et al. Heat shock promotes inclusion body formation of mutant huntingtin (mHtt) and alleviates mHtt-induced transcription factor dysfunction. The Journal of Biological Chemistry. 2018;**293**(40):15581-15593. DOI: 10.1074/JBC.RA118.002933

[113] Brown BE, Downs CA, Dunne RP, Gibb SW. Exploring the basis of thermotolerance in the reef coral Goniastrea aspera. Marine Ecology Progress Series. 2002;**242**:119-129. DOI: 10.3354/MEPS242119

[114] Barshis DJ, Stillman JH, Gates RD, Toonen RJ, Smith LW, Birkeland C. Protein expression and genetic structure of the coral Porites lobata in an environmentally extreme Samoan back reef: Does host genotype limit phenotypic plasticity? Molecular Ecology. 2010;**19**(8):1705-1720. DOI: 10.1111/J.1365-294X.2010.04574.X

[115] Desalvo MK, Sunagawa S, Voolstra CR, Medina M. Transcriptomic responses to heat stress and bleaching in the Elkhorn coral Acropora palmata. Marine Ecology Progress Series. 2010;**402**:97-113. DOI: 10.3354/MEPS08372

[116] Kenkel CD, Traylor MR, Wiedenmann J, Salih A, Matz MV. Fluorescence of coral larvae predicts their settlement response to crustose coralline algae and reflects stress. Proceedings of the Royal Society B: Biological Sciences. 2011;**278**(1718):2691-2697. DOI: 10.1098/rspb.2010.2344

[117] Rosic NN, Pernice M, Dove S, Dunn S, Hoegh-Guldberg O. Gene expression profiles of cytosolic heat shock proteins Hsp70 and Hsp90 from symbiotic dinoflagellates in response to thermal stress: Possible implications for coral bleaching. Cell Stress & Chaperones. 2011;**16**(1):69. DOI: 10.1007/S12192-010-0222-X

[118] Montalbetti E, Biscéré T, Ferrier-Pagès C, et al. Manganese benefits heat-stressed corals at the cellular level. Frontiers in Marine Science. 2021;**8**:1-14, 681119. DOI: 10.3389/fmars.2021.681119]

[119] Chow AM, Steel R, Anderson RL. Hsp72 chaperone function is dispensable for protection against stress-induced apoptosis. Cell Stress & Chaperones. 2009;**14**(3):253-263. DOI: 10.1007/S12192-008-0079-4/FIGURES/5

[120] Seveso D, Montano S, Maggioni D, et al. Diel modulation of Hsp70 and Hsp60 in corals living in a shallow reef. Coral Reefs. 2018;**37**(3):801-806. DOI: 10.1007/S00338-018-1703-0/FIGURES/4

[121] Downs CA, Kramarsky-Winter E, Woodley CM, et al. Cellular pathology and histopathology of hypo-salinity exposure on the coral Stylophora pistillata. Science of the Total Environment. 2009;**407**(17):4838-4851. DOI: 10.1016/J.SCITOTENV.2009.05.015

[122] Seveso D, Montano S, Strona G, Orlandi I, Galli P, Vai M. Exploring the effect of salinity changes on the levels of Hsp60 in the tropical coral Seriatopora caliendrum. Marine Environmental Research. 2013;**90**:96-103. DOI: 10.1016/J.MARENVRES.2013.06.002

[123] Thummasan M, Casareto BE, Ramphul C, Suzuki T, Toyoda K, Suzuki Y. Physiological responses (Hsps 60 and 32, caspase 3, H_2O_2 scavenging, and photosynthetic activity) of the coral *Pocillopora damicornis* under thermal and

high nitrate stresses. Marine Pollution Bulletin. 2021;**171**:1-10, 112737. DOI: 10.1016/j.marpolbul.2021.112737

[124] Seveso D, Montano S, Strona G, Orlandi I, Vai M, Galli P. Up-regulation of Hsp60 in response to skeleton eroding band disease but not by algal overgrowth in the scleractinian coral Acropora muricata. Marine Environmental Research. 2012;**78**:34-39. DOI: 10.1016/J.MARENVRES.2012.03.008

[125] Milne Edwards H. Histoire naturelle des coralliaires ou polypes proprement dits 3: 1-560. Paris: Librairie Encyclopédique de Roret; 1860

[126] Dana JD. Zoophytes. United States Exploring Expedition During the Years 1838-1842. Vol. 7. Philadelphia: Lea and Blanchard; 1846. pp. 1-740. 61 pls. (1846: 1-120, 709-720; 1848: 121-708, 721-740; 1849: atlas pls. 1-61). Available online at: http://www.sil.si.edu/digitalcollections/usexex/navigation/ScientificText/USExEx19_08select.cfm

[127] Barshis DJ, Ladner JT, Oliver TA, Seneca FO, Traylor-Knowles N, Palumbi SR. Genomic basis for coral resilience to climate change. Proceedings of the National Academy of Sciences of the United States of America. 2013;**110**(4):1387-1392. DOI: 10.1073/PNAS.1210224110/-/DCSUPPLEMENTAL

[128] de Lamarck J-BM. Histoire naturelle des animaux sans vertèbres. Tome second. Paris: Verdière; 1816. 568 pp. Available online at: http://www.biodiversitylibrary.org/item/47698

[129] Thompson DM, Van Woesik R. Corals escape bleaching in regions that recently and historically experienced frequent thermal stress. Proceedings of the Royal Society B: Biological Sciences. 2009;**276**(1669):2893-2901. DOI: 10.1098/RSPB.2009.0591

[130] Oliver TA, Palumbi SR. Do fluctuating temperature environments elevate coral thermal tolerance? Coral Reefs. 2011;**30**(2):429-440. DOI: 10.1007/s00338-011-0721-y

[131] Thomas L, Rose NH, Bay RA, et al. Mechanisms of thermal tolerance in reef-building corals across a Fine-grained environmental mosaic: Lessons from Ofu, American Samoa. Frontiers in Marine Science. 2018;**4**:434. DOI: 10.3389/FMARS.2017.00434/BIBTEX

[132] Angilletta MJ. Estimating and comparing thermal performance curves. Journal of Thermal Biology. 2006;**31**(7):541-545. DOI: 10.1016/j.jtherbio.2006.06.002

[133] McIlroy SE, Thompson PD, Yuan FL, Bonebrake TC, Baker DM. Subtropical thermal variation supports persistence of corals but limits productivity of coral reefs. Proceedings of the Royal Society B: Biological Sciences. 2019;**286**(1907):20190882. DOI: 10.1098/rspb.2019.0882

[134] Bairos-Novak KR, Hoogenboom MO, van Oppen MJH, Connolly SR. Coral adaptation to climate change: Meta-analysis reveals high heritability across multiple traits. Global Change Biology. 2021;**27**(22):5694-5710. DOI: 10.1111/GCB.15829

[135] Costanza R, de Groot R, Sutton P, et al. Changes in the global value of ecosystem services. Global Environmental Change. 2014;**26**(1):152-158. DOI: 10.1016/j.gloenvcha.2014.04.002

[136] Kleypas JA, McManus JW, Menez LAA. Environmental limits to coral reef development: Where do we draw the line? American Zoologist. 1999;**39**(1):146-159. Available from: https://academic.oup.com/icb/

article/39/1/146/124572 [Accessed: 06-07-2020]

[137] Perry CT, Larcombe P. Marginal and non-reef-building coral environments. Coral Reefs. 2003;**22**:427-432. DOI: 10.1007/s00338-003-0330-5

[138] Dellisanti W, Tsang RHLRHL, Ang P, Wu J, Wells MLML, Chan LLLL. Metabolic performance and thermal and salinity tolerance of the coral Platygyra carnosa in Hong Kong waters. Marine Pollution Bulletin. 2020;**153**:111005. Available from: https://www.sciencedirect.com/science/article/pii/S0025326X20301235?dgcid=author [Accessed: 02-03-2020]

[139] Fisher R, Bessell-Browne P, Jones R. Synergistic and antagonistic impacts of suspended sediments and thermal stress on corals. Nature Communications. 2019;**10**(1):1-9. DOI: 10.1038/s41467-019-10288-9

[140] Kavousi J, Keppel G. Clarifying the concept of climate change refugia for coral reefs. ICES Journal of Marine Science. 2018;**75**(1):43-49. DOI: 10.1093/ICESJMS/FSX124

[141] Duprey NN, McIlroy SE, Ng TPT, et al. Facing a wicked problem with optimism: Issues and priorities for coral conservation in Hong Kong. Biodiversity and Conservation. 2017;**26**(11):2521-2545. DOI: 10.1007/s10531-017-1383-z

[142] de Soares MO. Marginal reef paradox: A possible refuge from environmental changes? Ocean and Coastal Management. 2020;**185**:105063. DOI: 10.1016/J.OCECOAMAN.2019.105063

[143] Dixon AM, Forster PM, Heron SF, Stoner AMK, Beger M. Future loss of local-scale thermal refugia in coral reef ecosystems. PLOS Climate. 2022;**1**(2):e0000004. DOI: 10.1371/JOURNAL.PCLM.0000004

[144] Kroeker KJ, Kordas RL, Crim RN, Singh GG. Meta-analysis reveals negative yet variable effects of ocean acidification on marine organisms. Ecology Letters. 2010;**13**(11):1419-1434. DOI: 10.1111/j.1461-0248.2010.01518.x

[145] Darling ES, D'agata S. Coral reefs: Fishing for sustainability. Current Biology. 2017;**27**(2):R65-R68. DOI: 10.1016/J.CUB.2016.12.005

[146] McClanahan TR. Marine reserve more sustainable than gear restriction in maintaining long-term coral reef fisheries yields. Marine Policy. 2021;**128**:104478. DOI: 10.1016/J.MARPOL.2021.104478