Coral reef fishes in a multi-stressor world

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Chapter Outline

Coral reef fishes and the ecosystems they support represent some of the most biodiverse and productive ecosystems on the planet yet are under threat as they face dramatic increases in multiple, interacting stressors that are largely intensified by anthropogenic influences, such as climate change. Coral reef fishes have been the topic of 875 studies between 1979 and 2020 examining physiological responses to various abiotic and biotic stressors. Here, we highlight the current state of knowledge regarding coral reef fishes' responses to eight key abiotic stressors (i.e., pollutants, temperature, hypoxia and ocean deoxygenation, pH/CO_2, noise, salinity, pressure/depth, and turbidity) and four key biotic stressors (i.e., prey abundance, predator threats, parasites, and disease) and discuss stressors that have been examined in combination. We conclude with a horizon scan to discuss acclimation and adaptation, technological advances, knowledge gaps, and the future of physiological research on coral reef fishes. As we proceed through this new epoch, the Anthropocene, it is critical that the scientific and general communities work

Fish Physiology. https://doi.org/10.1016/bs.fp.2022.04.011

to recognize the issues that various habitats and ecosystems, such as coral reefs and the fishes that depend on and support them, are facing so that mitigation strategies can be implemented to protect biodiversity and ecosystem health.

1 Introduction

Coral reef fishes represent the most speciose assemblage of vertebrates on the planet today (Hixon and Randall, 2019) and continue to be the focus of myriad research programs, where studies are becoming even more essential as anthropogenic activities negatively affect coral reef ecosystems worldwide. Coral reef fish species numbers are estimated to be between 5000 and 8000, making up anywhere from 16% to 25% of all named, extant fishes (Victor, 2015). Coral reef fishes exhibit an array of body morphologies, fin arrangements, locomotory types, feeding strategies, physiological adaptations, and reproductive modes. They range in size from less than 50mm (e.g., the cryptobenthic species; Gobiidae and Blenniiformes; Brandl et al., 2018), up to 18m in the largest fish in today's oceans, the reef-associated whale shark (*Rhincodon typus*). Moreover, coral reef fishes have long been investigated across a multitude of—morphology, systematics, evolution, ecology, and conservation, to name a few—that integrate naturally with physiological research. Such integrative studies have been of particular, recent (i.e., 21st century) importance as well and key to addressing the effects of multiple environmental and anthropogenic stressors, not only on individual coral reef fish species and within particular taxa, but also on whole ecosystems. Undeniably, given the current epoch, the Anthropocene, where the dominant influences on the climate and environment come from human-based (i.e., anthropogenic) activities, there has never been a more important time to be researching coral reef fishes and how they respond to multiple, simultaneous, and often interacting stressors. We begin this chapter with an overview of the state of knowledge, for which we use a systematic literature search and bibliometric analysis to illustrate. We then provide case studies and discuss how the individual and combined stressors, ordered by their frequency of occurrence in the meta-analysis, affect coral reef fish physiology. We conclude with a horizon scan to discuss potential for acclimation and adaptation, technological advances, knowledge gaps, and the future of physiological research on coral reef fishes with implications toward conservation and protecting biodiversity and ecosystem health.

2 Current knowledge and trends over time

We conducted a systematic literature search to find studies investigating effects of (multiple) environmental stressors on the physiology of (sub-) tropical coral reef fishes. We collated studies examining physiological effects of abiotic stressors, including (1) temperature, (2) pH/CO_2, (3) hypoxia/deoxygenation, (4) salinity, (5) turbidity, (6) pollution, (7) noise, and (8) pressure and biotic factors, such as (9) predator threats, (10) prey abundance, (11) parasites, and (12) disease on coral reef fishes.

The optimal search strategy included separate search terms for each of the 12 factors and was librarian-verified at James Cook University (Townsville, Australia) (see Appendix for more details and the search terms used (Supporting Information in the online version at https://doi.org/10.1016/bs.fp.2022.04.011)). Results of the different searches were pooled, duplicates were removed, and then the remaining articles were manually checked for their relevance, and subsequently retrieved for bibliometric analyses. We included (i) original research (i.e., no reviews or meta-analyses) on subtropical or tropical coral reef fishes (i.e., based on Fishbase's environment classification), and (ii) studies that investigated a physiological metric. Inter-disciplinary studies were included if they helped gain mechanistic insight into physiological processes (e.g., molecular studies looking at gene expression patterns of enzymes or stable isotope analyses). Studies investigating highly mobile pelagic species that can occur on (sub-) tropical coral reefs (e.g., whale sharks, etc.) and studies examining the effects of fisheries and angling related stressors were excluded. Purely ecological field and laboratory studies (e.g., those reporting biting rates on benthos and plant material) were excluded; however, studies that experimentally examined feeding rates were included if the authors investigated the mechanistic relationship between a stressor and feeding frequency. Studies examining swimming performance and kinetics (e.g., acceleration, velocity) were included, but those examining purely behavioral metrics (e.g., boldness, habitat preference, and risk assessment trials) were excluded. In line with this, biotelemetry studies were only included if they also examined physiological parameters (e.g., body temperature, acceleration, etc.). Methodological studies were largely excluded. Furthermore, an overview of all existing multi-stressor studies was also created by checking each of the studies resulting from the search for the number and type of stressor investigated. The resulting articles were analyzed in R (R Core Development Team, 2018) using the R package "bibliometrix" (Aria and Cuccarullo, 2017).

In total, the search resulted in 875 scientific articles, of which 862 could be retrieved for further bibliometric analysis. All articles were generated over a 42-year period (i.e., 1979–2020, inclusive). Yet, only 67 of these studies were published in the first 20 years of this analysis (i.e., 1979–1998), meaning that approximately 92% of the studies have been published between 1999 and 2020. In fact, there were only four studies published before the 1990s after which, until the year 2000, an average of eight articles were published annually. Research outputs for studies examining these 12 stressors on coral reef fishes accelerated at the turn of the century (i.e., from 2000 onward), with an average of 38 related studies being published annually through 2020. There were a few global events related to coral reef health that occurred around this time, which may have catalyzed some of these studies. For example, the Great Barrier Reef (GBR, Australia) underwent mass coral bleaching (Fig. 1) due to marine heatwaves (MHWs) associated with ocean warming in 1998, 2002, 2006, 2016, 2017, and 2020, which had never before been documented in

FIG. 1 Blue-green and black axil chromis (i.e., *Chromis viridis* and *C. atripectoralis*; Pomacentridae) swimming among fully bleached coral (i.e., *Acropora* sp.) near Lizard Island, Australia, in the northern part of the Great Barrier Reef 1 week into the marine heatwave, February–March 2016. *Photo credit: J.L. Rummer.*

human history (Hughes et al., 2021). It is noteworthy that 93% of the studies assessing the effects of temperature stress (e.g., simulated ocean warming conditions or heatwave events) on coral reef fishes, including studies investigating more than one stressor, were published between 2001 and 2020.

However, only 29 studies investigated two of the aforementioned stressors in combination and no studies examined three or more stressors together. Therefore, multiple stressor studies represented only 3% of the literature (Fig. 2). The most common combination for these dual-stressor studies included temperature and CO_2/pH, further highlighting the emphasis on climate change stressors (e.g., ocean warming and acidification) throughout the analysis (see Section 4). Of all the studies assessed, 52% examined one of the eight aforementioned abiotic stressors, and 45% examined one of the four biotic stressors (Fig. 2). Studies examining the effects of pollutants on coral reef fishes dominated the literature (i.e., 29% of all studies), which also represented the most examined of the abiotic stressors, followed by temperature (i.e., 13% of all studies) (Fig. 2). Of the biotic stressors, prey abundance was the most examined, representing 26% of all studies (Fig. 2) (see Appendix for further details (Supporting Information in the online version at https://doi.org/10.1016/bs.fp.2022.04.011)).

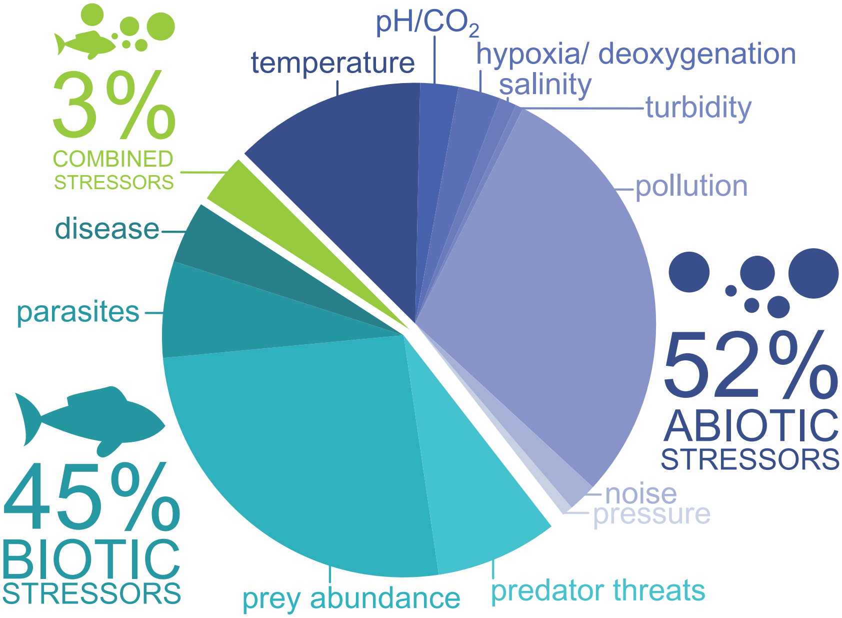

FIG. 2 Visual representation of the proportion of studies investigating the physiological effects of abiotic (i.e., temperature, pH/CO_2, hypoxia/deoxygenation, salinity, turbidity, pollution, noise, and pressure), biotic (i.e., predator threats, prey abundance, parasites, and disease) and combined stressors on coral reef fishes from 1979 to 2020, inclusive. Data were derived from 875 studies obtained from a systematic literature analysis (see Section 2).

Trends in research topics, assessed through the studies' author keywords, shifted over time (Fig. 3A). Several terms, such as stable isotopes, mercury, bioaccumulation, and foodwebs, occurred more frequently from 2016 onward, suggesting physiological metrics being used for examining feeding ecology and dietary shifts (see Section 3.2.1) as well as bioaccumulation and biomagnification of pollutants (see Section 3.1.1). A network analysis generated three main clusters of author keywords and visualized how the terms were connected (Fig. 3B). The most dominant keywords in the first cluster were fish, mercury, bioaccumulation, and biomagnification, with nine other minor keywords in this cluster, again, suggesting considerable emphasis on abiotic stressors associated with pollutants (see Section 3.1.1). The second cluster was dominated by keywords including stable isotopes, coral reefs, food web, and elasmobranchs, with seven other minor keywords, suggesting that biotic stressors associated with predator-prey relationships and food availability were heavily emphasized and perhaps most so on elasmobranch species, as shark was also one of the minor keywords. The third cluster was dominated only by two phrases: coral reef fish and climate change, with the other 18 keywords weighted similarly and most associated to climate change stressors like ocean warming and the various approaches that are used in physiological

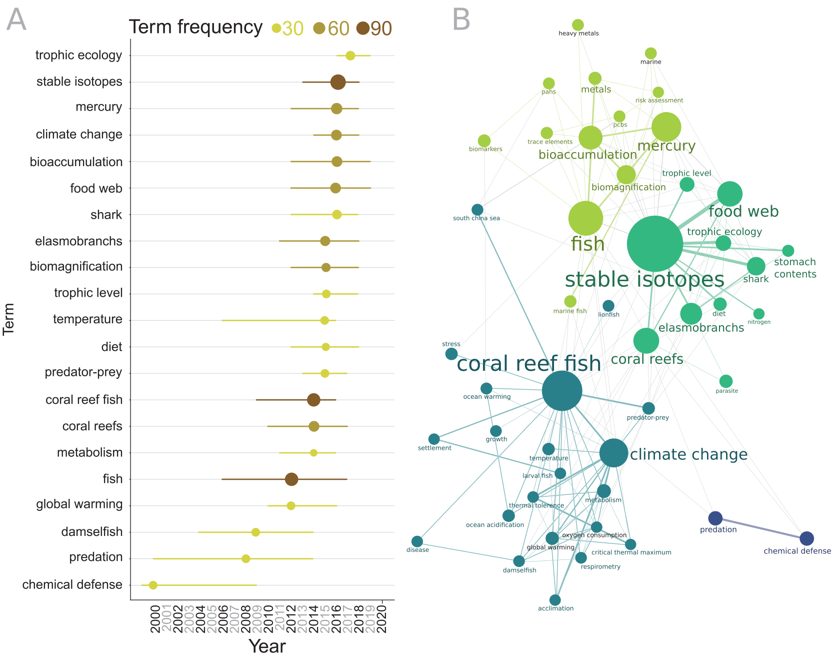

FIG. 3 The trend over time (A) and network analysis (B) of keywords (author generated) that were most frequently used to describe studies examining the physiological effects of various abiotic and biotic stressors on coral reef fishes. In panel A, the size of the circle represents the frequency (i.e., 30, 60, 90 times, and corresponding spectrum from yellow, to gold, to rust colors) by which the term was used as a keyword. While bibliometric results were derived from 875 studies spanning 1979 to 2020, due to the low number of studies prior to 2000, only keywords from 2000 to 2020 (x-axis) are represented here. In panel B, each circle represents a node, with the size of the node emphasizing the frequency by which the term is used. The nodes are connected by lines that represent edges, with the weight of the lines emphasizing the strength of the connection. The color map represents clusters or aggregations of nodes and edges. Together, the network of nodes and edges and where they aggregate depicts the relationships between terms. See Section 2 for more details.

studies to assess the effects of those stressors (e.g., respirometry, critical thermal maximum, etc.) on coral reef fishes. There was a fourth, minor cluster containing only two keywords: predation and chemical defense. Of these, predation was most frequently utilized as a keyword in 2008; whereas, chemical defense peaked as a keyword in 2000 (Fig. 3). The trends in keyword use have also seemingly shifted over time, with those most commonly using terms related to ocean warming, climate change, and elasmobranchs peaking in the last decade, which also reflects the trends described above (Fig. 3).

3 Stress in coral reef fishes (primary, secondary, and tertiary responses)

Classically defined, stress is "the nonspecific response of the body to any demand made upon it" (Selye, 1973); yet, the word "stress" invokes an array of definitions depending on the context and discipline. Here, stress is defined as the collective responses at primary, secondary, and tertiary levels underpinned by physiological mechanisms but often supported by behavioral changes that are key to re-establishing and maintaining homeostasis and ultimately surviving and thriving under an altered condition (Barton, 2002). A fish will respond to a threatening situation, the stressor, whether the threat originates abiotically or biotically, and whether physical, chemical, or perceived, via initiating a stress response. Therefore, it is the stressor that evokes the stress response. Primary responses are largely neuro-endocrine in nature via the hypothalamic–pituitary–adrenal (HPA) axis and involve a suite of catecholamines and corticosteroids (glucocorticoids) that are released into circulation (Wendelaar Bonga, 1997; see Chapter 3, Volume 39A: Castro-Santos et al., 2022). Secondary responses involve the initiation of heat shock proteins (HSPs) and changes in hematological parameters that instigate changes at the metabolic, cardio-respiratory, immune, and ion-balance levels (Mommsen et al., 1999). Primary responses can initiate secondary responses, and therefore, the relationships can be difficult to separate. Whereas, tertiary responses are often more behavioral and whole-organism level, resulting in changes in growth, movement, and decreased disease resistance, to name a few, and often stem from primary and secondary responses (Wedemeyer et al., 1990). The stress response can be immediately beneficial (e.g., fight or flight) or adaptive over the longer term, which is important to note given the classic definitions and misconceptions that stress is always negative (Chrousos, 1998). However, some stress responses may also be maladaptive, for example, considering responses that alter growth, feeding, digestion, immune function, and/or reproduction (Barton and Iwama, 1991). Despite the considerable variation across taxa and life history stages, the hormonal underpinnings of the stress response and resulting mechanistic responses are relatively well-understood and have been examined extensively across the teleost fishes, albeit less so in the elasmobranchs. The effects of multiple stressors, however, are not well-understood but are more relevant to the fishes—coral reef fishes or otherwise—today, living in the multi-stressor world of the Anthropocene.

3.1 Abiotic stressors (natural and anthropogenic)

Abiotic stressors arise from non-living influences on living organisms and can originate from chemical or physical sources and can be both natural and anthropogenic in origin, as well as originate both locally and globally. The order of the following sections is based on the frequency of studies investigating the respective stressors in the bibliometric analysis. The most pervasive, individual abiotic stressors include pollutants (i.e., including heavy metals and other toxicants), temperature, low oxygen (i.e., hypoxia, deoxygenation), changes in pH or CO_2 (often communicated together), noise, salinity, pressure or depth, and turbidity.

3.1.1 Pollutants

Toxicology studies on coral reef fishes have a long and extensive history, with some of the first physiological studies commencing at least by the 1970s (reviewed in Wood, 2012; also see Chapter 3, Volume 39B: De Boeck et al., 2022). While much is known regarding the effects of various metals and their bioaccumulation capacities, emerging pollutants (e.g., poly-aromatic hydrocarbons (PAHs), polychlorinated biphenyls (PCBs), flame retardants (e.g., polybrominated diphenyl ethers, PBDEs, and polybrominated biphenyls, PBBs), surfactants, and pesticides and interacting stressors are a product of the Anthropocene. The foundational work in these early toxicology studies, however, has been key in integrating and assessing the effects of emerging pollutants such as micro- and nano-plastics (reviewed in John et al., 2021), antibiotics and other pharmaceuticals, and although not unique to the Anthropocene, the increased prevalence of ciguatoxins (CTXs). Yet, it is important to note that, even though the physiological effects of heavy metal exposure have been thoroughly investigated over the years, with technological advancements (e.g., computers, smartphones, smartwatches) and their rapid turnover rates and associated waste issues, metal pollution has remained a pervasive issue.

Heavy metals largely come from agricultural, technological, medical, and industrial sectors are categorized by whether they are biologically essential or nonessential to the organism. Biologically essential metals include copper (Cu), zinc (Zn), chromium (Cr), nickel (Ni), cobalt (Co), molybdenum (Mo), and iron (Fe), and while these metals have known biological roles, toxicity can occur if concentrations are too low or too high. In contrast, nonessential metals, such as aluminum (Al), cadmium (Cd), mercury (Hg), tin (Sn), and lead (Pb) have no demonstrated biological function in fish, and so toxicity tends to commensurate with concentration. Due to increased heavy metal demand in the Anthropocene and issues associated with runoff, effluent discharge, and atmospheric fallout, heavy metal distribution in coastal waters has become widespread. Sea ports, having concentrated economic and recreational activities, have long been recognized as environments that are susceptible to heavy metal pollution. In Queensland, Australia, for example, there are 21 ports ranging from small community, multi-cargo, and multi-national coal export terminals, all of which are in close proximity to the Great Barrier Reef, meaning that coral reef fishes are highly susceptible to heavy metal exposure, and as such have been heavily investigated.

Heavy metals tend to accumulate in fish as they feed and respire, with consequences throughout other physiological systems, such as the liver, due to its metabolizing and detoxifying properties. Metals are also well-known inducers of oxidative stress as well, and so many studies have examined oxidative damage (reactive oxygen species, ROS, production) and antioxidant defenses (e.g., superoxide dismutase; SOD, catalase; CAT, glutathione peroxidase; GPx, and glutathione-s-transferase; GST) in fish species exposed to metals (reviewed in Sevcikova et al., 2011). Yet, the earliest studies were likely executed because vertebral deformities were observed in fish exposed to cadmium. The different pathways of accumulation lead to differential distribution of heavy metals across the various tissues of the fish but can also be influenced by the presence of metallothioneins (i.e., primary metal-binding proteins), the metabolic activity of the particular organ or tissue, the rate of blood flow, and metal-specific binding properties. While many studies on heavy metal exposure/accumulation in coral reef fishes have taken a mechanistic perspective and spanning developmental stages, much focus has been for applied outcomes. This is likely given the proximity of heavy metal sources and recreational and commercial fishing sectors and the potential for bioaccumulation in economically prized species (e.g., coral trout, *Plectropomus* spp.). As such, many coral reef fish species—and specific tissues, such as the liver—have become bioindicator species for harmful levels of heavy metals (e.g., Great Barrier Reef, Rayment and Barry, 2000), and this area of research will be important in addressing the effects of interacting stressors.

The demand for petroleum products has increased dramatically since the mid-20th century, with oil extraction and transport activities growing. More than 6 million metric tons of petroleum products have entered the oceans, largely due to industrial discharge, urban run-off, and shipping operations, and more than 300 major marine oil spills since the 1970s (summarized in Johansen et al., 2017). The heavy crude oils that are a key component of these processes include PAHs that are toxic, carcinogenic, mutagenic, and teratogenic to marine life (Negri et al., 2016). Because PAHs come from many sources—pyrogenic (combustion-derived) and petrogenic (petroleum-derived)—are often lipophilic, and break down slowly, they are pervasive in the marine environments, especially near urban areas, industrial or shipping operations and oil drilling/extraction sites. Yet their effects on coral reef fish species, trophic transfer, and potential for bioaccumulation (over ontogeny) and biomagnification (across trophic levels) are still not well understood.

While many studies on PAH exposure in coral reef fishes come from an applied, human health angle (i.e., consumer driven), further researchers have started investigating potential adverse health effects for the fish as well. Liver and bile metabolites, enzymes, and muscle tissue are typically analyzed across species, ontogeny, trophic levels, and source proximity to determine bioaccumulation, biomagnification, and if/when species would be good bioindicators (Juma et al., 2017; De Albergaria-Barbosa et al., 2017). Indeed, such analytical approaches determined that PAH contamination in coral reef fishes from the South China Sea originated from biomass combustion, petroleum sources, and vehicular emissions (Li et al., 2019). Similar to those associated with antioxidant roles with metal exposure, enzymes that have been specifically identified for tracking PAH exposure because of their elimination pathways include ethoxyresorufin-O-deethylase (EROD) and GST (Cullen et al., 2019; King et al., 2005). It has also been determined that liver burdens are indicative of acute exposure to PAHs because the tissue is highly dynamic when compared to muscle. However, muscle burdens are useful to assess chronic exposure because of the slower turnover rate and lower likelihood of concentrating such contaminants due to lipid mobilization. Invasive species (e.g., lionfish, *Pterois volitans*) have been used as biomonitoring species with PAH accumulation via biomarkers including bile fluorescence and liver enzyme activities (Van Den Hurk et al., 2020). Two economically valued Australian reef-associated species, the gold-spotted trevally (*Carangoides fulvoguttatus*) and bar-cheeked coral trout (*Plectropomus maculatus*), have also been used as bioindicators (King et al., 2005). Yet, such studies continue to highlight that, factors such as the fish's lipid content, length, and weight can affect PAH accumulation (Jafarabadi et al., 2019, 2020; Sun et al., 2019). Trophic ecology is key as well, with sharks prone to bioaccumulation and biomagnification since they occupy high trophic levels in their ecosystems. Although Cullen et al. (2019) measured higher than expected PAH accumulation in the liver and muscle samples from several shark species, they also noted that diet, niche partitioning, and life history characteristics, including those spanning ontogeny, affect PAH accumulation.

It is known from studies on PCBs that PAH accumulation results in similar adverse health effects in fishes, such as, but not limited to decreased vitamin A concentrations, thyroid hormone deficiency, and immunosuppression. PAH exposure also alters growth and has a suite of other physiological effects as demonstrated in salmonids (e.g., Meador et al., 2006), cod (Sørensen et al., 2019), haddock (Meier et al., 2010; Sørhus et al., 2016), herring (Incardona et al., 2012) and mahi mahi (Mager et al., 2017). Other studies have indicated that PAH exposure and accumulation in fishes can cause genotoxicity (and associated carcinogenesis), as well as endocrine and metabolic disruption (reviewed in Cullen et al., 2019) and enhanced photo-toxicity upon exposure to ultra-violet (UV) radiation (Aranguren-Abadía et al., 2022). While the interaction with PAH and UV exposure has been thoroughly demonstrated in cod (Aranguren-Abadía et al., 2022) and mahi mahi (Alloy et al., 2016), given the proximity of coral reefs to UV radiation and the surge of studies documenting adverse effects of PAH and UV exposure on corals (Overmans et al., 2018), it follows that this combination of stressors will continue to increase in relevance in the Anthropocene. Early life history stages of coral reef fishes may be most vulnerable as well, as determined by Johansen et al. (2017) in six pre-settlement stages of coral reef fishes, where PAH exposure resulted in greater mortality, stunted growth rates, altered habitat settlement, and changes in anti-predator behaviors (reduced sheltering and shoaling and increased risk-taking). Such results suggest a novel path of PAH injury whereby higher-order cognitive processing and behaviors necessary for successful settlement and recruitment of larval coral reef fishes are impaired (Johansen et al., 2017). More work is needed, and this will be an area of research on coral reef fishes that will continue to increase in importance and necessity.

Environmental levels of PCBs and various organochlorin-based pesticides (e.g., dichlorodiphenyl trichloroethane; DDT) have been on the decline (e.g., Rachel Carson's *Silent Spring* was published in 1962, and both were banned in the United States in the 1970s and other countries soon after), but many fish species still exhibit significant levels. This is likely because their overall toxicity, capacity for bioaccumulation and biomagnification (Kobayashi et al., 2019), low elimination (Wang and Wang, 2005) in fishes, long half-lives, continued use in some areas (e.g., DDT for malaria control in Kenya), and prevalence in landfills, sediments, and rivers mean that they remain in marine ecosystems. Studies like those examining the effects of PAH exposure on fishes have been executed to determine the effects of PCB and DDT exposure, but perhaps for longer, since the advent of modern agriculture and industrial pesticides. Moreover, because there is a relationship between, for example, PCB exposure time and age, some coral reef fish species (e.g., *Abudefduf sordidus*, blackspot sergeant; Kerr et al., 1997) have been used as bioindicators. Much work has incorporated trophic positions using various organisms (e.g., phytoplankton, copepods, and fish; Wang and Wang, 2005) to determine trophic magnification factors of such environmental pollutants (e.g., benthic food webs compared to pelagic food webs; Kobayashi et al., 2019). While much of this research is executed because of the implications these pollutants have on human health when persisting in marine ecosystems, these compounds also directly affect the physiological health of coral reef fishes (e.g., including sharks and rays, Storelli et al., 2011; Cullen et al., 2019). Most effects are at the level of endocrine pathways (e.g., steroid biosynthesis, oogenesis, spermatogenesis, etc.), and liver is the tissue most often analyzed (reviewed in Reijnders and Brasseur, 1997; Storelli et al., 2011). Climatic and ecological factors, temperatures, rainy versus dry seasons, etc. can affect how such compounds degrade or persist in marine environments (Wandiga et al., 2002), and given that they persist despite bans, this area of research will likely continue to be important.

Emerging pollutants such as, for example, micro- and nano-plastics will continue to pose health concerns for coral reef fishes and their ecosystems, given their global abundance and persistent use, even as single-use, by humans. The sources of these plastics and why they end up in the oceans (i.e., and more specifically why there are more micro- and nano-plastics in shallow, productive areas, such as coral reefs) are clear (Jambeck et al., 2015). Yet, exposure is seemingly unavoidable, especially under the current global waste management and production trends. Models predict that, by 2050, 12,000 million tonnes (MT) of plastic waste will be incinerated, 9000 MT will be recycled, and 12,000 MT of waste will be disposed of in landfills or in the natural environment (reviewed in John et al., 2021). Moreover, it is not just the chemical composition (e.g., polypropylene, polyethylene, polypropylene ether, polyethylene terephthalate, polyester, etc., all of which have been well-studied in terms of their toxicity), but also the chemical additives, which are often used to improve the structural properties of the plastic, that also contribute toxic effects (Galloway et al., 2017). While the size of micro- and nano-plastics is key, as it is within optimal prey ranges for many organisms in the marine environment, the shape and color also influence ingestion rates and toxicity (Galloway et al., 2017). Like with other pollutants, bioaccumulation via ingestion and transfer across trophic levels is the starting point, and studies commencing in the early 2000s through to the present emphasize that microplastics can now be found at every trophic level (Kroon et al., 2018). However, the mechanisms that underpin transfer from digestive tissues across to other organ systems are not yet clear. From freshwater fish models, studies have determined that nano-plastic particles can cross the blood-brain-barrier, which may underpin behavioral issues observed upon exposure (Mattsson et al., 2017). And, when coupled with the stress of degraded habitat, coral reef fishes (e.g., Ambon damselfish, *P. amboinensis*) that ingest micro-plastics, exhibit bold, risk-taking behaviors that decrease survival, which may relate to their nutritional status (McCormick et al., 2020). Given that another study found no effect of micro-plastic ingestion on settlement stage surgeonfish (*Acanthurus triostegus*) when faced with the threat of predatory lionfish (*Pterois radiata*) (Jacob et al., 2019), it is clear that more work is needed in this area, especially when considering that coral reef fishes exposed to increasing concentrations of micro- and nano-plastics will also be facing other stressors in concert. Although plastic toxicity has been studied for decades, this is an emerging stressor coral reef fishes are experiencing and one they will continue to face if waste management protocols remain unabated.

3.1.2 Temperature

Temperature is one of the most well-studied abiotic stressors in coral reef fishes, second only to pollutants. Whether warm or cold temperatures, over acute or chronic timescales, the physiological effects of thermal stress on most ectotherms, including the coral reef fishes, are generally understood. Moreover, with increasingly pervasive MHWs and widespread warming due to climate change, contemporary studies focus heavily on temperature. However, the temporal scale and the magnitude over which temperature changes occur, the order in which certain physiological systems respond to thermal stressors, and how those physiological responses affect behavior, movement, distribution, and other fitness-relevant traits will depend on species, life history stage, prior thermal history, and the presence of other stressors.

Physiological sensitivity to changing temperatures can commence at the most basic level but the mechanistic underpinnings are not always easy to interpret. Ectotherms in general, coral reef fishes included, typically exhibit an increase in biochemical rate functions with an increase in temperature. This temperature quotient or Q_{10} relationship, on average, suggests that for every 10 °C increase in temperature, rates double or triple (i.e., $Q_{10}=2–3$; Clarke and Johnston, 1999; Schmidt-Nielsen, 1997). Classic examples of these relationships come from studies on enzyme activities and organ tissue preparations (e.g., muscle contractions) under controlled laboratory conditions (Fields and Somero, 1997; Gelman et al., 1992; Johns and Somero, 2004; Johnson and Johnston, 1991; Lin and Somero, 1995). In contemporary studies, this relationship is also often reflected in estimates of metabolic rates (e.g., standard, resting, active, and maximum), where species compensating for a temperature increase can maintain Q_{10} at or around 2 (Eme and Bennett, 2009a), while those unable to compensate exhibit Q_{10} relationships well exceeding 2 (Rummer et al., 2014). Trade-offs may occur as well, where compensation occurs for functions at rest but not under maximal performance, or energy is saved in one trait at the cost of another, which may depend on the behavior and functional role of the species (Johansen and Jones, 2011; Rummer et al., 2014).

Several theories have been proposed to predict the causes of the various physiological responses to compensate (or not) for temperature increases. The Gill-Oxygen Limitation Theory (GOLT) proposes that body size and function in fish is limited by the gills' inability to adjust and supply sufficient oxygen to satisfy increasing metabolic costs under elevated temperatures (Pauly, 2019). The Oxygen and Capacity Limited Thermal Tolerance (OCLTT) hypothesis proposes cardio-respiratory transport and tissue demand as the main determinants of an organism's performance under ocean warming (Pörtner, 2014; Pörtner et al., 2017). However, mixed empirical evidence has led to a controversy about the exact mechanisms affecting species' performance under elevated temperatures, as none of the current theories can explain all observed responses (reviewed in Audzijonyte et al., 2019; Ern et al., 2017; Jutfelt et al., 2018). More broadly unifying principles are currently lacking (but see Audzijonyte et al., 2019; Clark et al., 2013; Ern, 2019). Reviews on this topic have, therefore, emphasized the urgent need for cross-disciplinary, mechanistic studies that explore the timescales over which thermal responses occur to assess the molecular and physiological mechanisms underpinning temperature compensation, especially in thermally sensitive species (Audzijonyte et al., 2019; Jutfelt et al., 2018).

Coral reef fishes, given their latitudinal distribution, especially populations living in particularly low latitudes (i.e., closer to the equator), are likely adapted to narrow temperature ranges (i.e., stenothermal, as opposed to eurythermal). This suggests that, despite living in warmer climes than their temperate latitude counterparts, coral reef fishes will exhibit greater sensitivity to temperature increases associated with ocean warming as they are already living close to their upper thermal limits (Eme and Bennett, 2009b; Rummer et al., 2014; Tewksbury et al., 2008). For example, five species of coral reef fishes from three latitudinally distinct populations spanning more than 2300 km from the southern Great Barrier Reef to near-equatorial locations of Papua New Guinea exhibited no differences in optimal temperatures for aerobic performance (Rummer et al., 2014). This was despite the equatorial populations residing in a very narrow range (e.g., approximately 2 °C) and the southern Great Barrier Reef populations residing in a much wider range (e.g., approximately 10 °C) of annual, seasonal temperatures (Rummer et al., 2014), suggesting a wide thermal buffer zone for high latitude populations and high temperature sensitivity in the near-equatorial populations. This is not unprecedented either with loss of hypoxia tolerance (Nilsson et al., 2010), increased metabolic costs (Gardiner et al., 2010; Rodgers et al., 2018, 2019), reductions in swimming performance (Johansen and Jones, 2011), and worsened predator escape responses (i.e., slower reaction times, slower escape speeds, and shorter escape distances; Allan et al., 2015; Motson and Donelson, 2017; Warren et al., 2017) when compared to their control temperature counterparts. Although these trends in coral reef fishes have only been revealed since the early 21st century, this topic has been historically well-researched in terrestrial species (Deutsch et al., 2008; Tewksbury et al., 2008).

Many examples of temperature sensitivity in coral reef fishes exist, and factors such as latitude/biogeography, activity level, and size (Di Santo and Lobel, 2016, 2017; Messmer et al., 2017; Ospina and Mora, 2004), help determine temperature sensitivity. Interestingly, in equatorial populations of two damselfish species, calculated Q_{10} values for resting metabolic rate estimates at 29 and 34 °C well exceeded $Q_{10}=2$ (i.e., 4.8 and 7.2), suggesting that, at 34 °C, over twice as much energy is required for these species to maintain routine metabolic processes than at their summer average temperatures of 29 °C (Rummer et al., 2014). It could be that the high Q_{10} values are a product of the stable, narrow thermal range experienced by these small, tropical, coral reef fishes residing near the equator. Likewise, two closely related coral reef fish species (*Abudefduf vaigiensis* and *A. whitleyi*) exhibited different energetic costs upon exposure to cooler temperatures, which resulted in reduced growth rates, feeding rates, burst escape speed and metabolic rates that were more pronounced in the species with the narrower latitudinal range (Djurichkovic et al., 2019). Species with wide thermal ranges (e.g., *A. vaigiensis* in the former example), however, have the potential to expatriate into new habitats, suggesting that climate-driven range shifts could result in species introductions and alter trophic interactions and predator-prey dynamics (Barker et al., 2018; Figueira et al., 2019; Rowe et al., 2018). Life stage may play a role as well. Given that the majority of coral reef fishes have a bipartite life cycle, consisting of a pelagic larval stage, many species could be venturing several hundred kilometers from their natal reefs and for weeks to months at a time in vastly different thermal regimes, thereby necessitating thermal compensation. However, if coral reef fishes are locally adapted to their thermal environment, do not regularly experience seasonal temperature fluctuations, and do not move far from these microhabitats, there would be no drive to possess such metabolic compensation for changes in temperature (e.g., acclimation or acclimatization, also see Section 5), further underpinning their temperature sensitivity as warming continues.

Indeed, understanding such temperature compensation strategies is also important when disentangling the responses of an organism upon acute changes (e.g., MHWs, Fig. 1; Allan et al., 2015; Bernal et al., 2020; Johansen et al., 2021) from how an organism responds to slowly increasing but chronically elevated temperatures (e.g., as with ocean warming). By definition, MHWs, which are when temperatures are warmer than the 90th percentile based on a 30-year historical baseline period and last for five or more days (Hobday et al., 2016), have been of particular concern on coral reefs, as heatwaves have been increasing in severity and frequency since the beginning of the 21st century. The rate of temperature increase may be important as well, as found in laboratory studies on coral reef fishes (Illing et al., 2020), but aside from a few studies (e.g., Allan et al., 2015), MHW scenarios have only been applied to coral reef fishes since coral reefs started bleaching (Fig. 1), globally, due to climate change mediated ocean warming (Hughes et al., 2021). Upon simulation of MHW conditions (e.g., 3 °C above ambient), two coral reef fish species (e.g., *Caesio cuning* and *Cheilodipterus quinquelineatus*) elicited coordinated responses in 13 tissue and organ systems over 5 weeks (Johansen et al., 2021). The onset and duration of biomarker responses (e.g., red muscle citrate synthase and lactate dehydrogenase activities, blood glucose and hemoglobin concentrations, spleen somatic index, and gill lamellar perimeter and width; Johansen et al., 2021), differed between species as well. The more active, mobile species (*C. cuning*) initiated responses to the simulated heatwave within the first week of exposure (Johansen et al., 2021). However, the more sessile, territorial cardinalfish species (*C. quinquelineatus*) exhibited a comparatively reduced response that was delayed over time. Perhaps the more mobile species, that would normally move to more favorable thermal microhabitats in the face of a MHW, once unable to do so instigated responses right away. In contrast, the more sessile species may be more prone to "wait it out" before initiating physiological responses. The study identified seven biomarkers, including red muscle citrate synthase and lactate dehydrogenase activities, blood glucose and hemoglobin concentrations, spleen somatic index, and gill lamellar perimeter and width, that proved critical in evaluating the progression as to how fish responded over the course of the simulated heatwave (Johansen et al., 2021). Some work has emphasized the role of gill biomarkers (Madeira et al., 2017a; Rodgers et al., 2019) or antioxidant chaperones (e.g., catalase, ubiquitin, lipid peroxidase; Madeira et al., 2017a), but ultimately, the degree of thermal sensitivity depends on the trait examined.

At the molecular level, gene expression patterns can help to rapidly and thoroughly survey the physiological processes that are key to maintaining homeostasis during a thermal event, with a plastic transcriptional response indicating varying degrees of thermal tolerance (Bernal et al., 2020).

Such changes in gene expression patterns have been found to be species and population specific (Veilleux et al., 2018a), which may factor into activity, behavior, and home range (e.g., cardinalfishes). Populations from higher latitudes with wider thermal ranges have exhibited greater plasticity in gene expression patterns in response to simulated heatwave events when compared to their lower latitude counterparts (Veilleux et al., 2018a), which supports findings for whole organism physiological traits as well. Gene expression patterns may also depend on the duration of exposure, as was found in wild coral reef fishes collected before, during, and after the MHW (Fig. 1) that was pervasive throughout the northern Great Barrier Reef in the austral summer of 2015–2016 (Bernal et al., 2020). Although it was the first time that gene expression patterns had been directly evaluated in wild fish populations during a MHW, it was perhaps not surprising that differentially expressed genes associated with immune function and cellular stress responses, including HSPs, mitochondrial activity, and toxin metabolism in the liver in response to the changing temperatures were uncovered (Bernal et al., 2020), given the physiological traits that have been assessed in previous studies. Other changes that were species-specific and temporally evident were related to fatty acid and cholesterol metabolism and glucose levels that may also be associated with secondary stressors these coral reef fish populations experienced during the MHW (e.g., changes in food availability and trophic interactions, increased algal cover) (Bernal et al., 2020). This is not unprecedented, however, as Norin et al. (2018) determined that, for orange-fin anemonefish (*Amphiprion chrysopterus*), the combination of warming conditions and resulting habitat damage (i.e., bleaching of their symbiont sea anemones; *Heteractis magnifica*) resulted in a significant increase in metabolic costs, which, over the longer term can lead to stress-induced changes to reproductive hormones and decreased fecundity (Beldade et al., 2017). Indeed, findings so far have emphasized the complex role of multiple stressors and cascading effects they will have on coral reef fishes as we move through the Anthropocene.

Certainly, many studies examining temperature stressors in coral reef fishes have done so within a life stage and population. Species or populations with narrow thermal ranges and those that do not experience dramatic changes in seasonal temperatures may not possess considerable capacity for thermal acclimation. In contrast, species or populations residing in more subtropical or temperate latitudes with greater seasonal variation in temperatures may acquire more tolerance for warm temperatures during the summer months and more cold tolerance (i.e., while losing high temperature tolerance) during the winter months (Fangue and Bennett, 2003). For example, low latitude populations of *Acanthochromis polyacanthus* exhibit increases in gill pathologies not found in mid or high latitude populations of the same species upon acclimation to elevated temperatures emphasizing thermal specialization in low latitude populations (Rodgers et al., 2019). Yet, in the pan-tropical clownfish species (*Amphiprion ocellaris*), thermal preference, tolerance, and aerobic metabolic scope were all found to depend heavily on acclimation (Velasco-Blanco et al., 2019), and similar findings were reported for subtropical *Hippocampus erectus* (Mascaro et al., 2019)—noting that both are important species in the aquarium trade. Acclimation or acclimatization may play a substantial role in how species respond to changing temperatures, which varies by species, population, and/or may depend on demography (Eme and Bennett, 2009b).

While acclimation can confer plasticity in some performance traits, it may not be the most reliable indicator of the ultimate survival and distribution of stenothermal coral reef fishes, especially the more mobile species, under ocean warming scenarios. Thermal preference and behavioral (e.g., movement) thermoregulation (Barker et al., 2018; Gervais et al., 2018; Habary et al., 2017; Hight and Lowe, 2007; Reyes et al., 2011; Speed et al., 2012b) can often supersede acclimation in some instances. Indeed, physiological thermal sensitivity and thermoregulatory behavior are likely coadapted (Angilletta et al., 2002, 2006; Huey and Bennett, 1987) as the thermal history that defines a species' optimal temperatures for performance (e.g., metabolic traits, swimming, etc., as discussed above) often determines its preferred temperature range as well (Bryan et al., 1990; Johnson and Kelsch, 1998). Therefore, in the wild, most species will likely pursue temperatures that coincide with their optimal performance temperatures during a given life stage (Beitinger and Fitzpatrick, 1979; Brett, 1971; Payne et al., 2016; Pörtner and Farrell, 2008; Pörtner and Knust, 2007). Critically, for behavioral thermoregulation to help mitigate the effects of rapid climate change, evolutionary changes in optimal temperatures for certain traits should also provide a strong selective pressure for changes in preferred temperatures (Angilletta et al., 2002; Bryan et al., 1990). This inherent relationship has been examined more frequently throughout contemporary studies in coral reef fish species with the aim of predicting phenotypic shifts in temperature sensitivity of various physiological performance traits (e.g., see Donelson et al., 2011, 2012) that may also lead to changes in preferred temperatures—such relationships may be the primary driver escalating the poleward migration of species. Indeed, current evidence suggests that 365 different species across 55 families of tropical fishes are either on the move or have already undergone bio-geographical redistributions or range shifts as a result of climate change and more specifically ocean warming (Feary et al., 2014; Figueira and Booth, 2010; Gervais et al., 2021).

3.1.3 Hypoxia and ocean deoxygenation

Oxygen is the greatest factor limiting physiological performance and survival of marine life, including the coral reef fishes (Sampaio et al., 2021). Nearly all vertebrate life requires oxygen (O_2) to support and sustain aerobic activities, and while anerobic (i.e., without O_2) metabolism is possible, it is time-limited and species- and context-dependent. Because O_2 is the final electron acceptor in the electron transport chain, O_2 partial pressures (pO_2) set the rates of aerobic metabolism. Aerobic metabolic rates are both dependent and independent of environmental pO_2 along a continuum; species that regulate metabolic rate independent of environmental pO_2 are referred to as "oxyregulators," and species whose metabolic rates conform to environmental pO_2 are referred to as "oxyconformers" (Mueller and Seymour, 2011). While most species are thought to be oxyregulators (Svendsen et al., 2019), and maximum metabolic rates in fishes (and ectotherms in general) are reduced with decreasing environmental pO_2, such rates do not increase when environmental pO_2 exceeds saturation (Seibel and Deutsch, 2020). Instead, standard metabolic rate (i.e., the energetic costs required to sustain basic metabolic functions) is regulated until pO_2 is too low, and fishes transition from oxyregulating to oxyconforming (see Fig. 1 in Heinrich et al., 2014).

Hypoxia is usually defined when dissolved O_2 concentrations fall below 2.8 mg O_2 L^{-1} (Breitburg et al., 2018), but this is an arbitrary threshold, because hypoxia tolerance is species- and context-specific, at the very least. It is also important to note that oxygen uptake is driven by the partial pressure gradient of the gas between the water and the blood, and therefore the associated parameters that determine oxygen solubility (e.g., temperature, salinity, pressure, etc.) are key. Species may also respond differently depending on life stage, energetic demands, and habitat conditions.

Most coral reef fishes, due to a bipartite life cycle, transition from a pelagic larval stage where they may spend weeks to months in the pelagic environment to settling onto the reef. In the pelagic, they exhibit record aerobic swimming and O_2 uptake capacities (Downie et al., 2021). Upon settling onto the reef and on into adulthood, however, reef fishes acquire notable hypoxia tolerance (Nilsson et al., 2007). Other species that mouth brood also exhibit unparalleled levels of hypoxia tolerance (Ostlund-Nilsson and Nilsson, 2004; Takegaki and Nakazono, 1999). Indeed, hypoxia tolerance may be a necessity for coral reef fishes to benefit from sheltering within the reef matrix at night because nighttime O_2 levels decrease dramatically (i.e., below 20% air saturation) when coral and other benthic organisms transition from photosynthesis to respiration (Nilsson et al., 2007; Nilsson and Ostlund-Nilsson, 2004). Moreover, small reef flats and tidepools that become isolated during low tide will also become hypoxic at night, necessitating hypoxia tolerance (Rummer et al., 2009). Several studies have assessed the capacity for coral reef fishes, from settlement to adulthood, to tolerate varying levels of hypoxia and the potential underlying physiological mechanisms (Nilsson et al., 2007; Nilsson and Ostlund-Nilsson, 2004). This is particularly interesting from a purely physiological perspective, such as hemoglobin (Hb) O_2 binding affinity. Usually, if an organism has a high capacity for O_2 delivery (low Hb-O_2 affinity) that would come with elite aerobic performance, they will not also have a high capacity for enhanced O_2 uptake (high Hb-O_2 affinity), which is usually observed in hypoxia tolerant species. This could change with life history stage, however, as was demonstrated with the salmonids in the late 1970s (Giles and Vanstone, 1978), or with hypoxia exposure (Bianchini and Wright, 2013). Indeed, several larval coral reef fishes have the highest mass-specific maximum O_2 uptake rates of any larval teleost (i.e., also any other ectothermic vertebrate measured) as well as the fastest swimming speeds for their body sizes (reviewed in Downie et al., 2021), suggesting high aerobic capacity during their larval life history stage. However, when coral reef fishes transition to the reef, they exhibit a dramatic decrease in critical oxygen tensions, suggesting they shift to being hypoxia tolerant (Nilsson et al., 2007). The reductions in aerobic metabolism and swimming performance that occur in coordination with settlement and hypoxia tolerance are seemingly unequivocal, but the exact timeline and underlying mechanisms are likely species-specific and not yet well-understood, but an area certainly warranting further investigation.

Beyond the teleost fishes, several elasmobranch species have been investigated for their typically uncharacteristic capacity to tolerate hypoxia and even anoxia (zero oxygen), which may also be related to the shallow, benthic, reef flat microhabitats that some shark species inhabit. In sharks, hypoxia initiates a suite of physiological responses, including ventilatory depression (Chapman et al., 2010) and expression of hypoxia inducible factor and heat-shock proteins (Renshaw et al., 2012). While several studies have investigated hypoxia and even anoxia tolerance in sharks and their relatives (reviewed in Pereira Santos et al., 2021; Rummer et al., 2022), only a few coral reef or reef-associated species have been investigated (e.g., Bouyoucos et al., 2020; Carlson and Parsons, 2001, 2003; Crear et al., 2019; Dabruzzi and Bennett, 2013; Hickey et al., 2012; Musa et al., 2020; Routley et al., 2002; Speers-Roesch et al., 2012; Wise et al., 1998). One such species is the epaulet shark (*Hemiscyllium ocellatum*), which has been the focus of the majority (i.e., at least 13 since the 1990s) of the studies on hypoxia and anoxia tolerance (in addition to studies on other environmental stressors) on sharks and their relatives. Unlike in other hypoxia- and anoxia-tolerant species, the epaulet shark exhibits no adenosine-mediated increase in cerebral blood flow and likely activates adenosine receptors that initiate metabolic depression and aid in maintaining brain adenosine triphosphate (ATP) levels—which would normally deplete—during an unprecedented 4h of anoxia (Renshaw et al., 2002; Söderstrom et al., 1999). Moreover, unlike other vertebrates, the epaulet shark preserves mitochondrial function—which would otherwise lead to cell damage and cell death—upon re-oxygenation post-anoxia exposure (Devaux et al., 2019). Given the small size of the epaulet shark and vulnerability to predation, it may make sense that this species exploits shallow, tidally influenced reef flats for shelter, even if such habitats exhibit dramatic declines in O_2. Therefore, this species must possess the physiological mechanisms that allow them to do so. Yet, it is interesting that these mechanisms used by the epaulet shark are different than what is understood for hypoxia tolerant teleosts and unprecedented in other elasmobranchs.

Despite the array of studies that have investigated low oxygen stress on teleost and elasmobranch fishes, no study published before mid-2021 has done so within a climate change context (i.e., ocean deoxygenation). It is important to clarify that the term hypoxia is not interchangeable with ocean deoxygenation (Klein et al., 2020), but quantifying hypoxia tolerance strategies and determining species' thresholds is important in defining the effects of ocean deoxygenation. This is especially important, given that hypoxia events elicit a stronger effect than ocean warming, ocean acidification, or the combination, and across biological traits (e.g., survival, abundance, development, metabolism, growth, and reproduction), taxonomic groups, ontogenetic stages, and climatic regions (Sampaio et al., 2021). Still, within the context of anthropogenic stressors, issues related to the effects of low oxygen on coral reef fishes have attracted far less attention in the scientific community when compared to other stressors (Sampaio et al., 2021).

Ocean deoxygenation is noted as the third global ocean syndrome but one that operates on different spatial and temporal scales than warming and acidification; yet, the term "ocean deoxygenation" was only first defined in 2009 (reviewed in Klein et al., 2020). Since the middle of the 20th century, the O_2 content of the oceans has decreased by more than 0.5–3%, low oxygen events (1–3.5 O_2 $\text{mg}\,\text{L}^{-1}$) are becoming more frequent and severe, and oxygen minimum zones (OMZs) are expanding (reviewed in Gregoire et al., 2021). While the causes are not fully understood, it is recognized that this process involves decreased O_2 and heightened biological consumption, which is worsened by enhanced stratification and induced by ocean warming. These changes, paired with rising ocean temperatures throughout the 21st century will further accelerate reductions in ocean O_2 content (reviewed in Gregoire et al., 2021; Klein et al., 2020).

3.1.4 pH/CO_2

Coral reef fishes are experiencing changes in water pH and CO_2 that stem from elevated atmospheric CO_2 ($p\text{CO}_2$; partial pressure) due to human-related emissions (ocean acidification; see above). Increased biological activity in shallow water habitats associated with coastal development and agricultural/industrial runoff can also contribute to elevated $p\text{CO}_2$, as can the ongoing global expansion of high intensity aquaculture (reviewed in Munday et al., 2019). While evolution suggests adaptations are in place for fishes to cope with such changes to maintain acid-base, ionoregulatory, and osmotic balance (reviewed in Hannan and Rummer, 2018; also see Chapter 5, Volume 39A: Eliason et al., 2022, and some extant fish species already live in elevated

$p\mathrm{CO}_2$ environments or experience them on a diel basis (e.g., coral reef fishes at night when corals shift from photosynthesis to respiration; Hannan et al., 2020a), laboratory experiments show different responses across species, life history stage, and exposure duration. Such differences in fitness-related traits, differential capacity for acclimation and/or adaptation, and the influence of multiple stressors will factor into predicting these impacts over the timescales at which CO_2 levels are rising.

Changes in environmental $p\mathrm{CO}_2$ and/or pH can dramatically affect the most basic most yet critical physiological processes in fishes—O_2 uptake, transport, delivery, and CO_2 removal, let alone ion and osmoregulatory processes (see Chapter 5, Volume 39A: Eliason et al., 2022). There is an intimate interaction between O_2 and CO_2 transport at the gills, and in other tissues, due to their interactions with Hb within the red blood cells (RBCs), which can vary by species (reviewed in Hannan and Rummer, 2018). Generally speaking, most cartilaginous fishes, such as sharks, skates, and rays, can efficiently compensate an acid-base disturbance due to the buffering capacity of their blood and plasma (Berenbrink et al., 2005). Moreover, most sharks, skates, and rays possess relatively pH-insensitive Hbs (Berenbrink et al., 2005), meaning that a pH disturbance associated with an acidosis, such as elevated $p\mathrm{CO}_2$, may not compromise O_2 transport in the way we understand for teleost fishes. Modern teleost fishes, such as the coral reef fishes, have a different physiological response to an acidosis than the cartilaginous fishes. Teleost fishes possess extremely pH-sensitive Hb—probably evolving nearly 400 million years ago (MYA) in basal Actinopterygians (reviewed in Randall et al., 2014)—and low buffering capacity in the blood and plasma. Adrenergically-activated transporters on the RBCs help to regulate pH, and plasma-accessible carbonic anhydrase in select locations enhances O_2 release from the tissues during an acidosis, such as elevated $p\mathrm{CO}_2$ (Randall et al., 2014; Rummer et al., 2013; see Fig. 1 in Hannan and Rummer, 2018). These traits result in an enhanced capacity for O_2 transport, especially during conditions that would normally preclude efficient O_2 uptake (Randall et al., 2014; Rummer et al., 2013). While these physiological traits may have facilitated the successful radiation of the fishes throughout geological history (Randall et al., 2014) and may be imperative in coping with ongoing and future changes in ocean $p\mathrm{CO}_2$, it is important to note that other morphological adjustments (e.g., gill remodeling) and physiological compensation mechanisms, such as bicarbonate-mediated ion exchange from the environment to correct extracellular pH (Deigweiher et al., 2008; Heuer and Grosell, 2014) are energetically expensive and may not be sustainable over the long term (Lefevre, 2016). Because extracellular pH compensation is limited by the amount of bicarbonate that can be exchanged (Brauner and Baker, 2009), teleost fishes can only tolerate and function in extremely high CO_2 conditions for a finite period. Indeed, work has been done in naturally high $p\mathrm{CO}_2$ conditions to understand the various mechanisms that underpin the physiological response to elevated pCO_2 conditions. For example, within the coral reefs near natural CO_2 seeps pCO_2 is similar to that predicted for the end of the century (i.e., ~1000 μatm; Munday et al., 2014). These seeps support diverse communities of coral reef fishes, yet fewer species occur near intense vents where pCO_2 ranges between 5000 and 10,000 μatm (reviewed in Munday et al., 2019). Therefore, these fish likely experience very high pCO_2 for short periods of time. Regardless of the exact mechanism, understanding how coral reef fishes perform at the physiological level under elevated pCO_2 may help in predicting ecosystem-level responses now and into the future.

Many of the adaptations potentially in place to maintain O_2 transport, CO_2 removal, and acid-base, ionoregulatory, and osmotic balance have been investigated in experimentally high pCO_2 settings and include hundreds of studies (reviewed in Hannan and Rummer, 2018). While a lot of these studies have focussed on more primitive and basal fishes and/or were for purely mechanistic understandings, there has been a surge of studies since the beginning of the 21st century investigating the physiological responses, acclimation processes, and adaptive capacity of coral reef fishes under ocean acidification relevant conditions. Such studies on coral reef fishes have spanned life history stages, species, activity levels, and habitats. Some of the first studies investigated larvae of the orange clownfish, *Amphiprion percula*, and the spiny chromis, *A. polyacanthus*. While elevated pCO_2 had no detectable effects on embryonic development, hatching time, or survival, let alone swimming performance, in orange clownfish, there were substantial increases in growth rates noted (Munday et al., 2009b). A study on spiny chromis also detected no effects of elevated pCO_2 in terms of growth or skeletal (i.e., otolith, ear bone) development (Munday et al., 2011a), which was surprising, as the basic chemistry associated with elevated pCO_2 and reduced carbonate saturation states would suggest an impact on bone calcification. However, exposure to much higher pCO_2 levels did result in larger otoliths in orange clownfish, which may be associated with increased acid-base regulation and increased precipitation of $CaCO_3$ (Munday et al., 2011b). It may be that coral reef fish species physiologically tolerate elevated pCO_2 levels because of the daily cyclic changes they already experience on the reef (Hannan et al., 2020a; Jarrold and Munday, 2018a,b). However, similar findings have been documented for large, highly mobile, pelagic, and widely distributed fish species as well, such as cobia, *Rachycentron canadum*, mahi-mahi, *Coryphaena hippurus*, and kingfish, *Seriola lalandi* (Bignami et al., 2013, 2014; Frommel et al., 2019; Laubenstein et al., 2018; Pan et al., 2020). Yet, these studies examined larval and juvenile stages of the pelagic species that likely also use shallow, nearshore habitats that would experience natural cycles of elevated pCO_2; however, when juvenile kingfish are reared under much higher, recirculating aquaculture system relevant pCO_2 levels, negative impacts on growth, swimming, and metabolism can be detected (Pan et al., 2020).

Studies on adults of reef-associated pelagic species are needed, as they are expected to be much more heavily impacted by elevated pCO_2 (Munday et al., 2016), but such studies are logistically challenging.

Other work on coral reef fishes has focussed on adult physiological performance and fitness-related behavioral traits in response to climate change relevant pCO_2 levels. Some of these results support the notion that teleost fishes can maintain aerobic performance under a mild pH disturbance, such as after short term exposure (e.g., weeks) to elevated pCO_2 conditions, possibly due to their unique capacity for maintaining O_2 transport (Rummer et al., 2013). These findings for maintained or enhanced performance (Couturier et al., 2013; Rummer et al., 2013) differ from the 47% decrease in aerobic scope observed in coral reef cardinalfishes exposed to similar CO_2 levels (Munday et al., 2009a). Yet, there may, indeed, be species specific differences (Couturier et al., 2013). Such differences may be related to when those species might be most active (diurnal vs nocturnal) and experiencing the highest pCO_2 levels in their natural reef habitats (exposure to constant elevated vs. fluctuating elevated pCO_2 levels) (Hannan et al., 2020a, 2020b, 2020c). For example, nocturnal cardinalfishes (e.g., *C. quinquelineatus*) have been found more sensitive to elevated, fluctuating pCO_2 levels (e.g., in terms of swimming and aerobic performance) than their diurnal counterparts (Hannan et al., 2021). Shallow water, benthic elasmobranchs such as the epaulet (*H. ocellatum*) and white spotted bamboo (*Chiloscyllium plagiosum*) sharks, as well as reef sharks that use shallow, lagoonal habitats as newborns (e.g., *Carcharhinus melanopterus*) exhibit minimal effects upon exposure to elevated pCO_2 conditions, even though elasmobranchs in general exhibit a slight yet significant negative response to ocean acidification relevant elevated pCO_2 conditions (reviewed in Rosa et al., 2017; Pereira Santos et al., 2021; Rummer et al., 2022). Some of these findings may be related to differences in physiological adaptations to maintaining performance under a mild acidosis, but various behavioral alterations as a result of exposure to elevated pCO_2 have been identified as well.

The physiological mechanisms underpinning altered behaviors (e.g., responses to alarm cues, behavioral lateralization, anti-predator responses (Allan et al., 2013), including fast-starts and reactions to chemical alarm cues, and sheltering), are likely related to acid–base regulatory processes interfering with γ-aminobutyric acid (GABA) receptor function (see fig. 4 in Schunter et al., 2018). The GABA-A receptor is the primary inhibitory neurotransmitter receptor in the vertebrate brain (Hamilton et al., 2014; Nilsson et al., 2012). Normally, ion gradients over the neuronal membrane result in an inflow of chloride (Cl^-) and bicarbonate ($HCO_3{}^-$) upon binding of the GABA-A receptor, which then leads to hyperpolarization and neuron inhibition. However, when fish are exposed to elevated pCO_2, pH compensation will change ion concentrations (see Fig. 1 in Hannan and Rummer, 2018) that could alter the receptor function and therefore could explain the behavioral changes that have been noted in coral reef fishes upon exposure to elevated $p\mathrm{CO}_2$ (Nilsson and Lefevre, 2016). Depending on the magnitude of changes in these ions during acid–base regulation, resultant alterations in ion gradients could either potentiate GABA-A receptor function or reverse its action, making it excitatory rather than inhibitory (Heuer and Grosell, 2014). Indeed, Heuer et al. (2016) were the first to pair some of the key behavioral assays with measurements of relevant intracellular and extracellular acid-base parameters in spiny chromis (*A. polyacanthus*) exposed to elevated $p\mathrm{CO}_2$. Even vision is related to GABA-A receptor function, as the negative effects of elevated $p\mathrm{CO}_2$ exposure on *A. polyacanthus* retinal function—where impairments could preclude a fish's capacity to quickly respond to threatening events—can be counteracted upon exposure to a GABA antagonist (Chung et al., 2014). Also, the effects of elevated $p\mathrm{CO}_2$ on fish behavior and sensory abilities occur when fish are exposed to levels >600 μatm $p\mathrm{CO}_2$, which is well within climate change relevant ocean acidification levels for the 21st century (Munday et al., 2010, 2012). Interestingly, few behavioral effects have been detected upon exposure to levels below 600 μatm and none below 500 μatm $p\mathrm{CO}_2$, which are levels that would resemble summer night time hours on most coral reefs (Hannan et al., 2020a). Therefore, behaviors (i.e., via acid-base regulation) may also be adapted to the daily fluctuations in $p\mathrm{CO}_2$ fishes experience within coral reefs, however, those behaviors could be sensitive to continuously elevated (as opposed to fluctuating) $p\mathrm{CO}_2$ conditions. Studies that link the timing of behavioral and acid–base regulatory responses to $p\mathrm{CO}_2$ fluctuations in coral reef environments have since been important in determining thresholds for ocean acidification relevant $p\mathrm{CO}_2$ levels and daily $p\mathrm{CO}_2$ fluctuations.

Understanding species-, context-, and temporally specific effects of elevated $p\mathrm{CO}_2$ on certain fitness-related traits is critical. However, molecular responses that underpin developmental, parental, and transgenerational effects of elevated $p\mathrm{CO}_2$ will be key in determining the long-term implications for coral reef ecosystem health. Predicting the potential for acclimation and adaptation cannot be done by acutely exposing animals to elevated $p\mathrm{CO}_2$ for days to weeks alone. Moreover, conditions experienced early in life can affect—via developmental plasticity—how an organism responds to those conditions later in life, which can also be mediated epigenetically (Schunter et al., 2018). The environment experienced by the parents can also influence how offspring respond (Munday, 2014; Schunter et al., 2016). Indeed, studies investigating transgenerational effects of elevated $p\mathrm{CO}_2$ exposure demonstrate that metabolic performance and growth rates are recovered in juvenile fish when both parents and offspring are exposed to elevated $p\mathrm{CO}_2$ (Miller et al., 2012). Heritability can underpin variations in the responses that offspring exhibit in response to elevated $p\mathrm{CO}_2$, which may be based on parental environments and responses (Welch and Munday, 2017). In *A. polyacanthus*, altered gene expression for the majority of within-generation responses return to baseline levels following parental exposure to elevated $p\mathrm{CO}_2$ conditions, suggesting that both parental variation in tolerance and transgenerational exposure to elevated $p\text{CO}_2$ are crucial factors supporting the response of coral reef fishes to ocean acidification relevant conditions (Schunter et al., 2018). Indeed, long-term developmental and generational studies will be important in understanding the role of individual variation in how coral reef fish species respond to elevated $p\text{CO}_2$, which will collectively be key in understanding and predicting the effects of elevated $p\text{CO}_2$ on populations and their capacity to adapt (Vargas et al., 2017).

3.1.5 Noise

Sound pollution or anthropogenic noise in the marine environment may originate from boat noise (commercial shipping, fishing, cruise, and recreational motorboats), seismic testing, and pile driving, activities that have all increased dramatically since the Industrial Revolution due to urbanization, resource extraction, tourism, and transportation. Anthropogenic noise is changing natural soundscapes worldwide (Duarte et al., 2021). Near coral reefs, anthropogenic noise predominantly comes from boat noise and, as such, is becoming recognized in international legislation as a prevalent and increasing anthropogenic pollutant (International Maritime Organization, 2014). However, it is important to distinguish between frequencies of sounds that naturally occur on the reefs (i.e., and their importance to fish health) and in the marine environment (e.g., 20 Hz—15 kHz, the sounds of the reefs, snapping shrimp, fish calls ranging from popping, trumpeting, to banging sounds, and the crushing of coral by parrotfishes as they feed), from artificial sounds associated with noise pollution (Gordon et al., 2018; Simpson et al., 2005a).

The Great Barrier Reef, Australia, has been the setting for work investigating the effects of anthropogenic noise on coral reef fishes, spanning species, life stages, experimental approaches, and exposure simulations (Gordon et al., 2018). This site is highly impacted by anthropogenic noise, and increasingly so, with predictions that 0.5 million recreational motorboats will be using the GBR by 2040 (GBR Marine Park Authority outlook report 2014). Motorboat noise affects physiological processes in coral reef fishes that can impact parental care (Nedelec et al., 2017a), navigation (Holles et al., 2013), foraging (Voellmy et al., 2014), surviving a predator threat or predator avoidance (Simpson et al., 2016), and various aspects of morphological development (Fakan and Mccormick, 2019). The physiological mechanisms underpinning these impacts are likely via metabolic (Simpson et al., 2016) and endocrine pathways (e.g., androgen/glucocorticoid pathways) and may also interact with how fish species respond to additional anthropogenic stressors (Mills et al., 2020).

Some species may be more sensitive to detecting sound pressure and frequency than others (Colleye et al., 2016), and both preconditioning (Staaterman et al., 2020), exposure duration, and the timeline over which sound impacts a fish (Egner and Mann, 2005; Parmentier et al., 2009; Wright et al., 2005, 2011) are also important. While closely related damselfish species can respond differently to anthropogenic noise (Fakan and Mccormick, 2019), populations of the same species may also respond differently. For example, populations of *Halichoeres bivittatus* living in noisy areas had differing levels of baseline stress (measured as whole-body cortisol) than populations living in quiet areas (Staaterman et al., 2020). Indeed, the period of noise exposure matters as well, being brief or acute, or chronic (Holmes et al., 2017; Mills et al., 2020; Nedelec et al., 2016, 2017b; Staaterman et al., 2020). Moreover, some species (e.g., Ambon damselfish, *P. amboinensis*) may habituate or desensitize to boat noise over extended periods as well (Holmes et al., 2017). Timing of exposure and associated effects in coral reef fishes may also have a lot to do with development. Of the 100 families of coral reef fishes, 36 families are brooders. They lay their eggs within the reef matrix, and parents often guard these eggs, during which time boat traffic and other anthropogenic noise could influence developmental milestones. This is all assuming that coral reef fishes have developed auditory sensory organs sufficiently while still developing in the egg and upon hatching, which is likely species specific. However, it has been determined for two species so far (i.e., *Amphiprion melanopus* and *A. polyacanthus*) that the effects of noise pollution begin during embryogenesis (Fakan and Mccormick, 2019). Regardless, the developing embryos, upon hatch either stay on the reef (i.e., where they may continue to experience anthropogenic noise) or leave for the pelagic where they spend weeks to months. For those species with a pelagic larval stage, navigating back to the coral reefs (i.e., whether natal or new) to settle is a crucial component of life history and may involve cues, such as the sounds of the reef (Simpson et al., 2004). These critical life history stages, if affected, could not only impact proper growth, development, and settlement of coral reef fish species, but could also impact demography and distribution patterns and therefore ecosystem health (Fakan and Mccormick, 2019).

Various methods have been used to physiologically assess the effects of anthropogenic noise on coral reef fishes and under different simulated soundscapes. Approaches assessed various levels of the stress response and have used heart rate monitoring, stress hormone analyses, the Auditory Brainstem Response (Egner and Mann, 2005), and Auditory Evoked Potential (AEP) audiometry (Colleye et al., 2016; Parmentier et al., 2009). Indeed, via the primary stress response, exposure to anthropogenic noise can result in increased glucocorticoid levels in fishes (Mills et al., 2020; Staaterman et al., 2020). Via the secondary stress responses, exposure to anthropogenic noise can result in increases in blood glucose and hematocrit (Filiciotto et al., 2013), and metaboloic rates can be altered as well (Simpson et al., 2005b; Staaterman et al., 2020). Indeed, Simpson et al. (2005b) and Jain-Schlaepfer et al. (2018) used changes in the secondary stress response (i.e., heart rate) to assess the acoustic sensitivity of early life stages of coral reef fishes. They found that clownfish embryos (*Amphiprion ephippium* and *A. rubrocinctus*) exhibit increased heartrate in response to noise, and their sensitivity increases across development from fertilization to near hatching (Simpson et al., 2005b). Via the tertiary stress response, exposure to anthropogenic noise can affect various aspects of movement (Holmes et al., 2017; Picciulin et al., 2010) that may be important for schooling and foraging as well as anti-predator behaviors (Simpson et al., 2015), parental care (Nedelec et al., 2017a; Picciulin et al., 2010), interactions between species (Nedelec et al., 2017b) and survival (Simpson et al., 2016). Studies often use playbacks of recorded sounds or real noise, which has been helpful in translating findings to management solutions. For example, exposure to the sound profile of a two- versus a four-stroke engine resulted in twice the stress response in *Amblyglyphidodon curacao* damselfish embryos, as measured by changes in heart rate (Jain-Schlaepfer et al., 2018) and twice the response at the level of escape performance in whitetail damselfish, *Pomacentrus chrysurus* (McCormick et al., 2019a). As a result, boat noise is starting to be included in environmental management plans as a stressor, and recommendations can be made regarding boat engine type based on empirical evidence. Anthropogenic noise is an area of research that will continue to grow into the Anthropocene.

3.1.6 Salinity

Salinity stress or iono- or osmo-regulatory stress (see Chapter 5, Volume 39A: Eliason et al., 2022) in relation to changes in environmental salinity have not been heavily investigated in coral reef fish species. Given that coral reef fish species are not as prone to such scenarios compared to estuarine and mangrove-dwelling species, this is expected. However, extreme scenarios do exist for coral reef fishes. For example, in areas such as the environmentally challenging Arabian/Persian Gulf, coral reef fish species (e.g., black-spot snapper, *Lutjanus ehrenbergii* and yellowbar angelfish, *Pomacanthus maculosus*) can incur the life-history and metabolic costs of osmoregulation in hypersaline environments, which are reflected in growth various parameters (D'Agostino et al., 2021). On a more temporal basis, reefs in some areas (e.g., Kaneohe Bay, Hawai'i) can succumb to storm flooding and freshwater inundation, making for hyposaline challenges and even mortality for resident fish species (Jokiel et al., 1993). Mechanistic studies (e.g., in the economically valuable coral trout, *P. maculatus* and *Plectropomus leopardus*, and also associated with capture stress; Frisch and Anderson, 2005) have been done including determining salinity preference (Serrano et al., 2010) and understanding the role of salinity in modulating reproductive hormones (Hung et al., 2010) and stress (e.g., heat shock proteins and cytoprotection; Tang et al., 2014a). In many cases, changes in gill morphology are observed, sodium potassium pump (Na^+, K^+, ATPase) activities and Na^+, K^+, $2Cl^-$ cotransporter proteins are measured and/or isoforms assessed to determine a coral reef fish's status in hypo- or hyper-saline conditions (Tang et al., 2014b). Studies have also been designed for applied outcomes, such as for streamlining aquaculture practices, understanding range expansions for invasive species (e.g., lionfishes; Jud et al., 2014; Schofield et al., 2015), and interpreting interactions with other stressors. It is important to note, however, that some coral reef associated species may use estuarine and mangrove habitats as nursery areas and may therefore experience salinity fluctuations (Prodocimo and Freire, 2001; Shirai et al., 2018). However, still, few studies have investigated these issues specifically in coral reef fish species.

3.1.7 Pressure/depth

Studies assessing pressure and depth relationships in coral reef fishes have been largely from a mechanistic perspective or an ecological perspective, with few if any evaluating pressure or depth as a pervasive anthropogenic stressor. Studies have assessed the role of pressure—and therefore depth—on various components of vision in four coral reef fish species, yellowstripe goatfish (*Mulloidichthys flavolineatus*), manybar goatfish (*Parupeneus multifasciatus*), convict surgeonfish (*Acanthurus triostegas*), and (orangespine unicornfish) *Naso lituratus*, and concluded a minor role of habitat depth with ocular transmission (Nelson et al., 2003). Other studies have assessed the role of depth or pressure in modulating the release of brain hormones important for circadian rhythms (e.g., including dopamine, serotonin, etc.), reproductive hormones (e.g., follicle stimulating and luteinizing hormones) and environmental cues such as time of day with respect to important ecological processes (e.g., spawning synchrony in threespot wrasse, *Halichoeres trimaculatus*; Takemura et al., 2010, 2012)). Indeed, reproduction seems to be the most sensitive to pressure and depth, but it is important to note that it may be challenging to disentangle the effects associated with depth from those related to light. Depth has a negative impact on ovarian development in the sapphire devil, *Chrysiptera cyanea* (Fukuoka et al., 2017). In contrast, an opposite relationship was found upon comparing bicolor damselfish (*Stegastes partitus*) between shallow (<10 m), deep shelf (20–30 m), and mesophotic (60–70 m) reefs. Populations were less dense, but individuals were older and larger on the deeper reefs with potentially longer life spans, a broader diet niche, and higher reproductive investments producing high condition larvae, when compared to shallow reefs (Goldstein et al., 2016, 2017). Indeed, there has been an eco-physiological component to these studies that, while not directly addressing pressure and depth as anthropogenic stressors, have investigated shifts and requirements for species distribution as habitat suitability declines with the continuing global loss of shallow water reefs.

3.1.8 Turbidity

Since the middle of the 20th century, many nearshore coral reefs have experienced decreasing water quality, in particular increasing turbidity and increasing concentrations of suspended sediments (often referred to as total suspended solids, TSS), due to coastal development, land conversion, mining, shipping, and dredging (Foley et al., 2005; Syvitski et al., 2005). Although often used interchangeably, often complementary, and both indicate the clarity of the water, turbidity and TSS measure different things. Turbidity examines at how well a light passes through liquid, while TSS is a quantitative expression of suspended particles. Indeed, increasing TSS concentrations are leading to changes in the composition of fish assemblages on coastal reefs (Bejarano and Appeldoorn, 2013; Cheal et al., 2013; Moustaka et al., 2018), either indirectly through changes in benthic composition and/or directly through impacts on the fishes themselves (Fabricius et al., 2005; Hamilton et al., 2017). Yet, the direct effects of TSS exposure and other sources of turbidity on the physiology of coral reef fishes have been seldom investigated, until recently.

Some of the most profound physiological effects of TSS exposure in coral reef fishes have been observed at the gills. Orange-spotted grouper (*Epinephelus coioides*) exhibit a decrease in gas diffusion distance at the gill in response to suspended sediment exposure (Wong et al., 2013). However, suspended sediments can also directly damage the gill epithelium. Studies found shortened gill lamellae (Hess et al., 2017; Lake and Hinch, 1999; Sutherland and Meyer, 2007), increased growth of protective cell layers, which increases gas diffusion distances (Cumming and Herbert, 2016; Hess et al., 2015; Lowe et al., 2015), and an increase in mucous secretion (Hess et al., 2015; Humborstad et al., 2006). Moreover, coral reef fishes exposed to elevated suspended sediment levels exhibit gill microbiome shift from "healthy" to pathogenic bacterial communities, which can further compromise immune function (Hess et al., 2015). All of these changes can reduce gas exchange efficiency and interfere with oxygen uptake across the gills (Evans et al., 2005; Lappivaara et al., 1995). That said, it may not be surprising that exposure to suspended sediments can decrease maximum oxygen uptake rates ($\dot{M}O_{2max}$) in juvenile anemone fish, *A. melanopus*, and increase resting oxygen uptake rates ($\dot{M}O_{2rest}$, a proxy for metabolic costs required to sustain basic metabolic functions) (Hess et al., 2017). These changes can reduce aerobic scope (i.e., difference between $\dot{M}O_{2max}$ and $\dot{M}O_{2rest}$) and thus overall capacity for aerobic activity. A reduction in aerobic scope can affect aerobic activities such as growth and development, with negative consequences for the survival and fitness of fishes (Norin and Clark, 2016). In contrast, however, two confamilial species, *A. percula* and *A. melanopus,* have been found to maintain aerobic performance, despite changes in gill morphology following suspended sediment exposure (Hess et al., 2017).

While the consequences of gill alterations to aerobic metabolism and performance may seem straightforward, the effects of suspended sediment exposure on anerobic metabolic pathways and performance traits are not as clear. Sediment-exposed coral reef fish species, such as juvenile anemonefish (*A. melanopus*) can respond faster to a mechanical stimulus, achieve higher escape speeds and acceleration, and escape further distances than their control counterparts (Hess et al., 2019). This kind of response counters what is expected when fish are exposed to other stressors (e.g., elevated temperatures). However, visual acuity is reduced for fishes living in turbid waters, which could also impact predator detection times. Therefore, the effects of suspended sediments on escape performance may be more related to the behavioral changes that are required as fish increase vigilance and perceived predation risk in turbid waters than direct effects of TSS on physiological mechanisms. Indeed, newly settled *Chromis atripectoralis* are preyed upon by an ambush predator, *P. fuscus*, much more heavily under medium suspended sediment concentrations (Wenger et al., 2013). It is important to note that the effects of suspended sediment exposure on aerobic metabolic pathways could impact a coral reef fish's capacity to recover from these anerobically driven responses. Increased vigilance can also increase metabolic costs due to trade-offs associated with activity and foraging (Killen et al., 2015). Over the longer-term, this could result in non-consumptive costs (e.g., compromised immune function, or reductions in growth and condition) (Hawlena and Schmitz, 2010). Regardless, predator escape performance plays an important role in predator-prey interactions, and any changes whether physiological, behavioral, or a combination of both, are likely to directly influence survival of juvenile and adult fishes on coral reefs (McCormick et al., 2018). Finally, it is important to note, like with many of the stressors affecting coral reef fishes today, seldom does one stressor occur in isolation (e.g., in the wild, TSS may contain pollutants; increased turbidity may co-occur with the warmest seasons and therefore elevated temperatures, flood plumes and storms; dredging and coastal maintenance and thus increased noise, etc.); therefore, their effects cannot be assumed independent from other abiotic or biotic influences—this is an area requiring much more investigation.

3.2 Biotic stressors

Biotic stressors arise from living organisms and can originate from natural and anthropogenic sources. The most pervasive, individual biotic stressors include prey abundance, predator threats, parasites, and disease.

3.2.1 Prey abundance

Changes in prey abundance—in some cases related to starvation, dietary shifts over temporal (e.g., ontogeny) and spatial scales, trophic interactions, resource partitioning, and food webs represent the largest biotic stressors studied in coral reef fishes. One of the most common approaches used to discern these relationships is via stable isotope analysis of bones and tissues. Stable isotopes of nitrogen, carbon, sulfur, and oxygen can be useful in determining trophic position of consumers and nutrient sources (i.e., linking consumers to their food sources; Speed et al., 2012a), influential factors in the environment (e.g., flow velocities, substrate type, amount of rainfall, and possibly temperature), oxidation/reduction conditions of certain habitats, and overall habitat use (Bouillon et al., 2008). Changes in certain stable isotopes over time can be useful in determining diet switching or habitat shifts. Moreover, because different tissues respond at different rates, they can provide a time history of diet and habitat use. The widely used stable isotope approach does not directly assess physiological stress in coral reef fishes. The approach can, however, help infer when there are resource-use overlaps and trophic redundancies in certain ecosystems, ecologically distinct regions, and can provide baseline information to help identify potential for fisheries pressure or other anthropogenic stress (e.g., in elasmobranchs; Morgan et al., 2020; Peterson et al., 2020).

Metabolic responses to different feeding regimes, starvation, digestion and assimilation rates (e.g., specific dynamic action; SDA) have been examined in many coral reef fish species. Such approaches may be especially important during the larval stage, with the extremely high mortality rates (see above) and rapid growth rates that require a large supply of planktonic prey (reviewed in McLeod and Clark, 2016). With increasing temperatures resulting from climate change, tropical marine plankton communities, which are the primary food sources for larval coral reef fishes, are predicted to shift in composition and distribution. This could very well result in a mismatch between coral reef fish larvae and their prey. Studies assessing metabolic costs to different food rations as well as determining the energetic budgets of different feeding regimes (e.g., *A. percula*, McLeod et al., 2013; McLeod and Clark, 2016) provide important information for assessing individual performance and predicting recruitment success and ecosystem health under various stressors. In controlled laboratory studies, this is an interesting avenue, given that many protocols feed experimental animals ad libitum, which could be masking the effects of other treatments (e.g., McMahon et al., 2018, 2019). Such food ration and feeding regime information are useful for applied outcomes as well, such as in ensuring efficient aquaculture practices and in understanding adverse effects of eco-tourism provisioning and other non-consumptive wildlife activities (Birnie-Gauvin et al., 2017). For example, in the Cook Islands, tourists often feed bread to threadfin butterfly fish (*Chaetodon auriga*) and striated surgeonfish (*Ctenochaetus striatus*), which results in reductions in their foraging on natural food sources (Prinz et al., 2020). Some reef sharks may shift their behaviors in response to long-term provisioning. For example, at a long-term provisioning site in French Polynesia, blacktip reef sharks (*C. melanopterus*) now exhibit smaller home ranges and have changed how they use their habitat (Mourier et al., 2021). Interestingly, after tourism activities ceased for six consecutive weeks (i.e., due to COVID-19 pandemic lockdowns in 2020), all animals left the area, and pre-lockdown abundances were not restored for at least 1 month after tourism resumed (Séguigne, 2022). However, some species exhibit no effect of provisioning at all, like Caribbean reef sharks (*Carcharhinus perezi*; Maljkovic and Cote, 2011) and juvenile lemon sharks (*Negaprion brevirostris*; Heinrich et al., 2020). In the latter species, provisioning neither affected spatial distribution nor mean daily activity or energy requirements, but lemon sharks did start exhibiting anticipatory behaviors as soon as 11 days following regular provisioning (Heinrich et al., 2020).

Dietary stress and the effects of food availability on trophic interactions can also be assessed via the microbiome, which, with the advent of high throughput sequencing, has become much cheaper, faster, and informative. Given the important role the gut microbiome has in nutrient acquisition and pathogen resilience, establishing baseline data and having a rapid means for determining dietary stress (e.g., as in surgeonfishes, Family Acanthuridae; Miyake et al., 2015) will increase in importance, especially with interacting anthropogenic stressors. Coral reef fish species inhabiting disturbed reefs have changes in gut bacterial composition and fermentative bacteria ratios, suggesting that this disturbance not only affects the gut microbiome community but also impacts ecosystem function through microbial processes (Cheutin et al., 2021). But moreover, coral reef fishes living in reefs characterized by high suspended sediment concentrations exhibit changes in gill microbiome as well, with implications toward immune function, metabolic performance, growth, and development (Hess et al., 2015). Indeed, this approach can also elucidate feeding stress in post-disturbance reefs (e.g., following coral bleaching, Fig. 1, or crown-of-thorns starfish outbreaks). Finally, if gastrointestinal microbial fauna, which is fundamental to fish health, is not flexible enough to accommodate new habitats and food sources (e.g., rabbitfish, *Siganus fuscescens*; Jones et al., 2018), this may be problematic as coral reef fish distribution patterns and ranges change due to ocean warming.

3.2.2 Predator threats

The primary ecological interaction between organisms that most significantly shapes selection and fitness is predation (i.e., eat, but do not get eaten); coral reef fishes are no exception. Because most coral reef fishes produce larvae that spend some portion of early life in the pelagic before settling onto new or natal reefs, predation is a serious threat. Settling juveniles are small and naïve (Almany and Webster, 2006); thus, the time around settlement can be a life-history bottleneck for coral reef fish populations due to predation mortality. Moreover, many coral reef fishes occupy low to mid trophic levels, meaning they are subject to piscivory through all life stages. While predator-prey dynamics represent naturally occurring stressors within coral reef ecosystems, continued human exploitation of reef predators, habitat degradation (i.e., nurseries, shelter; McCormick et al., 2019b), and additional stressors into the Anthropocene will potentially further alter coral reef fish population dynamics and ecosystem health.

While much work on predator threats has been from an ecological perspective, most predator-prey interactions have physiological underpinnings (Palacios et al., 2016). This includes vast array of body morphologies, color changes (e.g., mimicry, Cortesi et al., 2015), and chemical defenses (e.g., toxic gobies, Gratzer et al., 2015, but also toxins from other non-fish species, like polychaetes, sponges, soft corals, etc.). Predator-prey interactions, perhaps especially on coral reefs, also represents an area where non-consumptive effects (NCEs) have been well-investigated (Mitchell and Harborne, 2020). Indeed, NCEs due to the risk, fear, and other non-lethal interactions associated with predator-prey dynamics can change prey behavior, physiological performance, such as metabolism and swimming, morphology, and development, which may result in changes in distribution patterns and overall fitness (Arvizu et al., 2021; Hess et al., 2019; Mitchell and Harborne, 2020). Ultimately, most physiological underpinnings of predator-prey dynamics are associated with the primary (e.g., catecholamine release) and secondary (e.g., glucocorticoid release) stress responses and metabolic performance (e.g., escape responses). Glucocorticoids can cross the blood-brain barrier (e.g., unlike most catecholamines) and therefore interact with receptors in several brain regions meaning their role in the stress response is quite important in modulating behaviors (reviewed in Soares et al., 2012). Cleaning gobies (*Elacatinus evelynae*) release cortisol when encountering a "client" that could be a potential predator, but of the "fight," "flight," or "freeze" responses typically associated with stress, *E. evelynae* exhibits more of a "fight" response by cleaning more thoroughly and being more proactive, which may be an effort to reduce predatory danger or conflict (Soares et al., 2012). The metabolic and neurophysiology that underpins fast-start, escape responses and are triggered by an approaching predator include anerobically powered myotomal blocks of fast glycolytic muscle and Mauthner neurons in the brain (reviewed in Allan et al., 2013; Ramasamy et al., 2015). However, behavioral lateralization—the preferential use of one side of the body or another (Domenici et al., 2012)—is another trait that is key to predator escape responses (Ferrari et al., 2017). Escape performance in coral reef fishes, overall, has been well investigated in many species, and whether fast starts or lateralized movements, both reveal a high degree of inter, intra-specific and within-individual plasticity (Allan et al., 2013, 2014, 2015, 2017, 2020). Such capacity to modulate these responses may be beneficial given the "high cost of repaying O_2 debt" upon an exhaustive challenge and the metabolic (e.g., stress) and behavioral disruption associated with escape responses (Allan et al., 2015). Additional energy saving occurs, as coral reef fishes can discriminate between predator and non-predator, which can be detected in certain metabolic traits and honed with a history of predator exposure (Hall and Clark, 2016; Ramasamy et al., 2015). When juvenile spiny chromis (*A. polyacanthus*) are pre-exposed to visual or olfactory predator cues, they exhibit stronger escape response (i.e., reduced latency, increased escape distance, mean response speed, maximum response speed and maximum acceleration) than if they had no prior experience (Ramasamy et al., 2015). Although morphological and performance variables are most often measured in response to predator interactions, the behaviors associated with these traits ultimately have the strongest effects on survival (McCormick et al., 2017).

The larval life stage of coral reef fishes is challenging to investigate because of its narrow window of time; yet, this stage has been the focus of the majority of predation studies on reef fishes (Almany and Webster, 2006). Yet, traits developed during this phase—such as, but not limited to, growth rates, body condition, lipid content, swimming, boldness, and escape performance—influence overall survival (e.g., in Pomacentridae, Booth and Beretta, 2004; Hoey and McCormick, 2004; Figueira et al., 2008; Fuiman et al., 2010). Even while parents are guarding eggs, predator threats can alter maternal cortisol levels (e.g., in *Pomacentrus amboinensis*), which can influence larval morphology via stress responses (McCormick, 1998). Embryonic cinnamon clownfish, *A. melanopus*, while *in ovo*, that are exposed to conspecific chemical alarm cues or conspecific alarm cues combined with predator cues respond by modulating their heart rate. This response indicates that they can detect and react to cues suggesting a conspecific has been injured. Moreover, they can also use such information to learn about predation, all of which may influence development and behavior (Atherton and McCormick, 2015). Evidence also suggests a strong transgenerational (i.e., parental) effect of predator recognition exists in coral reef fishes (Atherton and McCormick, 2020). If coral reef fishes are continuously exposed to high-risk conditions, they exhibit behavioral and physiological antipredator traits that are important when faced with an actual predator interaction, suggesting a strong ontogenetic pre-conditioning role (Ferrari et al., 2015a). Indeed, plasticity in traits and "as needed" responses may be key for some species, as predation is not always strong enough, consistent in space or time, and not always unidirectional to result in genetic adaptations and may also promote greater resilience in species as habitats continue to change (i.e., habitat degradation) into the Anthropocene (McCormick et al., 2019b).

3.2.3 Parasites

Parasites remain poorly studied due to sheer numbers and their cryptic nature; yet, parasites constitute the majority of biodiversity found on coral reefs (Sikkel et al., 2018). Parasitic interactions in coral reef fishes are exacerbated in the Anthropocene due to habitat loss, water quality reductions, and top-level predator removal (Artim et al., 2020). Among coral reef fishes, species that are commonly cultured as ornamentals and key for the aquarium industry are subject to parasites, often due to high density holding and immune suppression. However, parasites also occur in the wild naturally. Classic examples include grooming and cleaning stations (Grutter et al., 2003). While the diversity of parasites that interact with coral reef fishes is largely unknown, estimates suggest that there could be as many as 20 different parasite species for every coral reef fish species on the Great Barrier Reef and New Caledonia (reviewed in Justine et al., 2012). With this high diversity of parasites ranging from various worms, (e.g., flatworms such as Turbellaria, Monopisthocotylea, Polyopisthocotylea, Digenea, and Cestoda; roundworms, such as Nematoda; thorny-headed worms such as Acanthocephala; segmented worms, such as Hirudinea), protozoans, copepods, and isopods, and the array of associated infection and removal strategies, it follows that there would also be a vast suite of physiological effects assessed in coral reef fishes.

The most common stress associated with parasitic interactions in coral reef fishes is documented as changes in growth and development, but immune suppression, reductions in reproduction, and other metabolic costs are common Indeed, when ectoparasitic isopods infect the five-lined cardinalfish, *Cheliodipterus quinquelineatus*, they experience reductions in growth (e.g., 20% decrease in body mass) and reproductive output (e.g., 42% fewer ova) (Fogelman et al., 2009). In other fish species, these ectoparasitic isopods cause reductions in aerobic scope and swimming performance, including reductions in fast starts (Allan et al., 2020; Binning et al., 2013; Östlund-Nilsson et al., 2005). While it has also been found that interactions between cleaner fishes and their clients may elicit pathogen transmission and disease transfer (reviewed in Narvaez et al., 2021), it is also important to note that cleaner fish interactions with their clients can also elicit benefits beyond parasite removal (e.g., tactile stimulation; Paula et al., 2015, and stress reduction; Paula et al., 2019).

Blood samples can be used to determine the degree of the immune response (e.g., leukocytes, granulocytes, etc.), blood loss (e.g., hematocrit), and hormone levels (e.g., cortisol, reproductive hormones; Allan et al., 2020), all of which can affect growth, aerobic performance, and reproduction (Demaire et al., 2020). Not only can these physiological effects be detected in the presence of a parasite, but such parameters may also represent trade-offs if the fish is unable to rid itself of parasites, for example, via the use of mutualistic cleaning stations (Demaire et al., 2020). Many ectoparasites that externally attach to their host fish can increase the drag of the host fish and therefore impact swimming and escape kinematics and behaviors, while increasing overall metabolic costs (e.g., bridled monocle bream, *Scolopsis bilineata*, Binning et al., 2013, 2014; Ambon damselfish, *P. amboinensis,* Allan et al., 2020). Effects of ectoparasites can vary by species and the size of the fish, among other factors, including diurnal as opposed to nocturnal species (Cook et al., 2015). For example, French grunt (*Haemulon flavolineatum*) and brown chromis (*Chromis multilineata*) are closely related species and both commonly infected by an isopod (*Anilocra* spp.), but the energetic effects (i.e., as per condition factor, percent moisture in the muscle tissue, total muscle tissue calories, and gut content volume) were different between species (Welicky et al., 2018), highlighting that such generalizations cannot always be made. Other infections can occur via consumption of an intermediate host. This is the case with blood flukes, which often enter fish hosts via polychaete worms. Adult blood flukes have been found in 26 species of butterflyfishes (Chaetodontidae) on the Great Barrier Reef, with fluke eggs observed in hearts and gills (Yong et al., 2013). Another example is in the ecologically and commercially important dusky grouper, *Epinephelus marginatus*, where histopathology revealed parasitic flatworms on the gills, resulting in inflammation and reduced immune function (Polinas et al., 2018). Indeed, much research has also focussed on the recreationally and commercially important coral reef barramundi (*Lates calcarifer*) as well, given its high value in aquaculture industry and the propensity for parasitic infections to interact with other environmental stressors (e.g., temperature and salinity; Brazenor and Hutson, 2015). Technological advancements in, for example environmental deoxyribonucleic acid (eDNA), are now making these outbreaks more detectable and predictable (Gomes et al., 2017). Undoubtedly, such energetic costs associated with parasite loads can be problematic on an array of levels, given that some ectoparasites infect their hosts for months to years. That said, parasites can greatly impact coral reef fish energetics and therefore population dynamics and ecosystem health. This biotic stressor will be continually examined, especially as it interacts with other biotic (e.g., disease) and abiotic (e.g., temperature, warming) stressors that are increasing in severity in the Anthropocene.

3.2.4 Disease

Novel pathogen exposure in coral reef fishes is increasing. However, not all diseases that are increasing in prevalence in coral reef fishes in the Anthropocene (e.g., carcinomas, melanomas from increased UV exposure, potentially due to ozone depletion) are from microbial exposure (i.e., from viruses, bacteria, and fungi). Indeed, disease prevalence in coral reef fishes is not a new topic. Rather, it has been a topic of intense investigation since the early 20th century, as many of the traditionally investigated diseases were common in coral reef fishes used in aquarium trades and human consumption (e.g., especially live trade). Today, stress, poor water quality (e.g., coastal development, sewage treatment issues, including an increased prevalence of pharmaceuticals in sewage, etc.), overcrowding (e.g., for cultured fish species), and runoff (e.g., industrial and agricultural) likely contribute to most of the diseases in coral reef fishes.

In cultured fish species (e.g., for food fish, ornamentals, aquarium trade, etc.), disease, whether viral, bacterial, or otherwise, represents a serious economic loss, but this could be the case for disease in wild fish species as well (e.g., fisheries, recreation, eco-tourism, etc.). Neurofibromatosis tumors or nerve sheath tumors (e.g., in bicolor damselfishes, *S. partitus*) may stem from a virus and can be fatal and is often associated with density issues (Fieber and Schmale, 1994; Schmale, 1995; Schmale et al., 2002, 2004). Some viruses (e.g., iridovirus) result in anemia and eventually spleen and kidney necrosis as well as general immunosuppression, which makes fish susceptible to other diseases (Mahardika et al., 2004). The hematopoietic necrosis virus, which originated in freshwaters species (e.g., the salmonids) but can now affect coral reef fishes, enters the fish from the base of the fins with the fish first exhibiting a bulging abdomen and eyes, and then external hemorrhaging commences, ultimately leading to mortality (Harmache et al., 2006). Another issue originating from a virus is hemorrhagic septicemia; the virus enters the fish via the gills, moves to the internal organs, and weakens the blood vessels, which eventually collapse, causing the hemorrhaging. However, septicemia can also come from bacterial infections and has been found to impact various reef-associated cartilaginous and teleost fish species (Briones et al., 1998; Camus et al., 2013; Keirstead et al., 2014). Natural outbreaks of *Streptococcus agalactiae*, which can be transmitted between humans and aquatic species, in wild groupers and various shark species have also resulted in many cases of septicemia (Bowater et al., 2012). As many pathogens can be transmitted between waterways via boats, trailers, and nets, some of these pathogens that originated in freshwater systems, probably in North America in the Pacific Northwest (i.e., likely via salmonids) or the Great Lakes, now impact coral reef fishes.

Density issues, eutrophic bodies of water, and pollution can underpin these bacterial infections and even result in tumor formation. Mycobacteriosis, for example, enters through open wounds or the gastro-intestinal system, spreads through the whole body of the fish via the circulatory and lymphatic systems, and can be rampant in many coral reef fishes, resulting in high mortality rates (Diamant et al., 2000). Evidence of melanoma in coral trout *P. leopardus* likely stems from increased ultraviolet radiation exposure (Sweet et al., 2012), which will continue to increase into the Anthropocene, especially in shallow water coral reef environments. Tumor formation can also come from chronic trauma, viral infections, or pollution as well as inbreeding and low genetic diversity. The latter can be most prevalent in the ornamental and aquarium fish trade while attempting to breed for certain traits (e.g., clown anemonefish, *A. ocellaris*). Odontomas are benign tumors of dental tissue and/or abnormal tooth formation that can lead to difficulties eating. Such tumors can also occur in the lips, gill arches, or esophagus as neoplasms or in the fat tissue as liposarcomas (Vorbach et al., 2018). Ultimately, the stressors that result in disease in coral reef fishes are becoming more prevalent and severe moving into the Anthropocene. Determining host ranges, timing, and environmental cues will be important in identifying the cause, source, or origin of the pathogen, potential pathogen habitat, how it might interact with other stressors, and how it can be best managed.

4 Interacting stressors

To date, the scientific community understands the least about the effects of combined (i.e., two or more) stressors on the physiology of coral reef fishes. Moreover, it is not always straightforward whether effects will be additive, synergistic, or antagonistic, or whether the combined effect of the stressors will equal, be greater than, or be less than the sum of their individual effects, respectively (see Gunderson et al., 2016 for review). The most common combination of interacting stressors that has been addressed has been ocean warming and acidification. Such studies found a decline in offspring quality in anemonefish, *A. melanopus* (Miller et al., 2015). In juvenile spiny chromis, *A. polyacanthus*, results suggest a negative correlation between behavioral (i.e., responding to an alarm odor) and physiological (i.e., aerobic metabolic scope) traits (Laubenstein et al., 2019). Moreover, such findings suggest the potential for trade-offs that limit fish performance and even the capacity for populations to adapt (Laubenstein et al., 2019). Combined warming and acidification conditions also negatively impact metabolic traits such as aerobic performance in two nocturnal cardinalfish species (*Ostorhinchus doedeleini* and *O.* cyanosoma; Munday et al., 2009a) and predator-prey kinematics and swimming performance in Ward's damselfish (*P. wardi*; Allan et al., 2017) from the Great Barrier Reef, Australia. Indeed, such combined stressors can affect behavioral traits that are key for predator-prey dynamics, but perhaps not unidirectionally (i.e., synergistically on overall predation rate, but antagonistically on predator selectivity; Ferrari et al., 2015b). Elevated temperatures in combination with elevated $p\text{CO}_2$ results in opposing effects in some traits, such as swimming performance (e.g., yellowtail kingfish, *S. lalandi*; Watson et al., 2018). Other studies have found neurobiological changes in response to the combined stressors in the form of dopaminergic and serotoninergic systems are important for cleaner fish species (e.g., *Labroides dimidiatus*) and their clients (e.g., *Naso elegans*); such cascading effects could impact community structures (Paula et al., 2019). While *in ovo*, embryonic bamboo sharks (*Chiloscyllium punctatum*) exhibit increased routine metabolic rates under the combined stressors of warming and acidification (Rosa et al., 2014). Upon hatching, juveniles exhibited decreased body condition (Rosa et al., 2014) as well as neuro-oxidative damage and loss of aerobic potential under such combined conditions (Rosa et al., 2016a). However, at 30 days post hatch, juveniles exhibited an antagonistic response to ocean warming and acidification conditions in terms of digestive enzyme activities (Rosa et al., 2016b), while metabolic costs increased and survival decreased (Rosa et al., 2014). Collectively, these studies demonstrate the importance of life stage, physiology, species, and habitat/life history strategies.

While these studies examining the combined effects of ocean warming and acidification relevant scenarios represent an important step in assessing and predicting the effects of climate change on coral reef fishes, they still lack the third primary abiotic stressor, being hypoxia and ocean deoxygenation. As discussed throughout this chapter, an array of experimental approaches simulating these scenarios have suggested potential sensitivities of coral reef fishes to any of these stressors in isolation, but we can only surmise the combination (Poloczanska et al., 2016; Richardson et al., 2012). Yet, this so-called "deadly trio" of ocean warming, acidification, and deoxygenation has been previously involved in some of Earth's mass extinction events (Bijma et al., 2013). Therefore, understanding how the physiological performance of coral reef fishes will be affected by climate change is of paramount importance. Despite the wealth of empirical data collected in the past decade, more advanced experimental approaches are needed to address existing knowledge gaps: the intraspecific variability in vulnerability to climate change stressors, the nature of the stressor interaction (e.g., additive, synergistic, or antagonistic), and the adaptative potential. The predicted co-occurrence of climate change stressors highlights the need for multi-stressor experimentation to realistically assess effects of climate change on coral reef fishes.

Ocean warming and prey abundance as interacting stressors has also been a topic of research priority, as increasing temperatures resulting from climate change are causing tropical marine plankton communities—the primary food sources for larval coral reef fishes—to shift in composition and distribution. Studies assessing metabolic costs to different food rations as well as determining the energetic budgets of different feeding regimes under different warming scenarios have been important steps to addressing this issue (McLeod et al., 2013). Newly hatched anemonefish, *A. percula*, exhibited decreased survival rates, and those that made it to settlement stage took longer to do so, longer to metamorphose, and exhibited lower body condition if they had been exposed to warm temperatures and low quantity diets (McLeod et al., 2013). These fish also exhibited higher energetic costs (i.e., via routine O_2 uptake rates) than their control counterparts, all of which suggests severe impacts of warming waters and declining food availability on larval coral reef fishes (McLeod et al., 2013). In adult breeding pairs of spiny chromis (*A. polyacanthus*) maintained under one of three temperatures and one of two feeding regimes, not only did elevated temperatures in isolation negatively impact reproduction and egg size, but none of the pairs reproduced under elevated temperatures and low quantity diets (Donelson et al., 2010). Trade-offs could occur to maintain one process over another, and therefore fitness, which could be seen in reproduction success and egg size/quality, as in Donelson et al. (2010), but also growth and immune responses. Moreover, in the wild, declining food availability may also result in fish spending more time and energy foraging, making them more vulnerable to predation. Indeed, this combination of stressors—elevated temperatures and decreased food availability—has already been examined within the context of predator (i.e., chemical alarm cue) recognition. Lemon damselfish, *Pomacentrus moluccensis*, while maintained under elevated temperatures and low food availability, not only depleted energy reserves and reduced growth, as expected, but were also unable to effectively elicit an anti-predatory response (Lienart et al., 2016). Only one study to date on a coral reef associated fish species has addressed the effects of elevated temperatures, reductions in food supply, and ocean acidification conditions and concluded that such conditions may increase starvation risk in larval cobia, *R. canadum* (Bignami et al., 2017).

While each of these 12 stressors (i.e., and others not discussed here) must be first understood in isolation, conclusions as to how coral reef fish species, populations, and ecosystems will be affected in the Anthropocene can only be drawn if multiple stressors are investigated together. Indeed, experiments that address combinations of global and local stressors (i.e., warming and turbidity/TSS, parasites and habitat degradation, noise and elevated $p\mathrm{CO}_2$, etc.) will be crucial. While it seems logical to emphasize the "deadly trio," local stressors are as damaging particularly when paired with global stressors. Undeniably, this is also further complicated when investigating an array of species with diverse life history strategies, across life history stages, and traits spanning various levels of biological organization. Effects of multiple stressors can be additive, synergistic, or antagonistic, and therefore if extrapolations are made based on the effects of just one stressor, whole organismal, species, population, and even ecosystem-level responses can be grossly underestimated or mis-represented. Indeed, multi-stressor experiments are the next step in predicting the impact of the Anthropocene on coral reef fishes and the ecosystems they support.

5 Acclimation and adaptation potential

Acclimation (or acclimatization), as nominally discussed earlier in this chapter as relevant to aforementioned stressors, and adaptation are the primary ways that organisms, such as the coral reef fishes, can survive and thrive under new environmental conditions. Addressing the potential for and limitations to acclimation and adaptation will be key research priorities for coral reef fishes in the Anthropocene.

Acclimation represents a type of phenotypic plasticity where one genotype has the capacity to express varying phenotypes when exposed to different environmental conditions (Angilletta, 2009). Phenotypic plasticity represents a rapid response mechanism (i.e., when compared to adaptation via selection for certain phenotypes) acting at the level of the individual (i.e., as opposed to populations) and may be key for organisms to respond to and survive changing environmental temperatures without genetic selection (Munday, 2014). Such "rapid" strategies may play a substantial role in compensation to new conditions, that is, if the new phenotype is beneficial. Yet, the capacity for acclimation also depends on the species, population, and/or its demography (Donelson and Munday, 2012; Eme and Bennett, 2009b) as well as prior history regarding environmental conditions (e.g., temperature; Angilletta, 2009). Developmental and transgenerational acclimation as well as epigenetic effects also play a role in how species respond to changes in their environments.

Early life-history traits and development are notoriously susceptible to altered environmental conditions, but in some cases, developmental acclimation can prime later stages for altered environmental conditions. It has been found that the thermal environment of the eggs (Gagliano et al., 2007), embryos, and juvenile early life stages—rearing temperatures—are important (Illing et al., 2020) and will affect the thermal tolerance traits of the adults

(Donelson et al., 2011). Increased rearing temperatures in cobia (*R. canadum*) results in decreased digestion efficiency (Yufera et al., 2019). When spiny chromis (*A. polyacanthus*) were exposed to elevated temperatures upon hatch and following hatch for set periods of time, those that were exposed to at least 30 days of elevated temperatures exhibited enhanced escape performance traits at this early life stage (Spinks et al., 2019). However, those with extended exposure (i.e., 108 days) to elevated temperatures exhibited reductions in body size, suggesting some trade-offs to long-term exposure and/or developmental windows that are more or less receptive to thermal history (Spinks et al., 2019). Developmental acclimation at the level of resting metabolic rates is also evident in newly settled lemon damselfish (*P. moluccensis*; Grenchik et al., 2012). Additionally, Donelson et al. (2011) determined that, while spiny chromis, *A. polyacanthus*, reared for their entire lives at temperatures that were 3 °C above ambient reduced their metabolic costs, they were also smaller and had poorer body condition than their control counterparts. In many species, early life stages exploit more thermally challenging habitats than adults, which may be for protection and/or resources, suggesting there is a perceived advantage of developmental plasticity (Dabruzzi et al., 2013; Bouyoucos et al., 2022); yet, some of these habitats and therefore species—especially at the edges of their thermal safety margins—might be most at risk under future climate scenarios (Madeira et al., 2017b).

The environment of the parents can also dramatically influence tolerance traits of the offspring (Donelson et al., 2012), and the molecular processes that underpin both developmental and transgenerational acclimation to various climate change stressors (e.g., warming) are becoming more and more clear (Veilleux et al., 2015). In some species (e.g., *A. polyacanthus*), paternal influence (e.g., fewer and poorer quality offspring) is more profound than maternal influence with regards to elevated temperatures (Spinks et al., 2021). In this example, such alterations could stem from the role stress has in regulating sex hormones. Non-genetic inheritance (i.e., epigenetic changes) can underpin various aspects of within-generation phenotypic plasticity in coral reef fishes (Ryu et al., 2020). Environmental history can also carry over for many generations, as has been demonstrated in spiny chromis (*A. polyacanthus*) where step-wise increases in temperature over generations can increase reproductive performance (Donelson et al., 2016; Veilleux et al., 2018b) and restore aerobic metabolic traits (Bernal et al., 2018). When parent cinnamon anemone fish, *A. melanopus*, were exposed to elevated $p\text{CO}_2$, their offspring (i.e., via non-genetic inheritance) exhibited improved escape performance, metabolic rate estimates, and growth, but benefits were not observed in all traits examined (Allan et al., 2014; Miller et al., 2012). Limitations to transgenerational acclimation were also noted in juvenile spiny damselfish, *A. polyacanthus*, from parents exposed to elevated $p\text{CO}_2$, in terms of olfactory preferences and behavioral lateralization (Welch et al., 2014). While the presence of rapid, developmental and transgenerational acclimation still necessitates environmental preferences and behaviors (Donelson et al., 2012), it will buffer coral reef fish populations against the challenges of climate change and other anthropogenic stressors over the short term. However, it is important to note that, although transgenerational acclimation may provide offspring with increased tolerance to challenging environmental conditions, very few of the studies that have been executed to date have been truly transgenerational; studies have been generally conducted with one generation of progeny, despite the primordial germ cells of that generation being exposed when the parental generation is exposed to such conditions, which is a topic worthy of future investigation. Non-existent or even incomplete developmental or transgenerational acclimation for coral reef fishes living in the changing waters of the Anthropocene necessitates genetic adaptation.

Where acclimation can occur over relatively short time scales, adaptation typically requires many generations and therefore, depending on the species, much longer time frames. That said, the way in which various forms of acclimation interact with adaptation are still not understood and will be the focus of research in the coming decades. Research questions centering around how acclimation can shift mean phenotypes, and thus the strength or direction of selection, without genetic change as well as how selection acts on traits expressed by phenotypic plasticity, and whether changes in phenotypes can become decoupled from changes in genotypes are at the forefront (reviewed in Munday, 2014). The role of epigenetic variation is also factored as well, as non-genetic inheritance, although considered for decades, has only just been detailed under this umbrella. Indeed, when compared to genetic inheritance, epigenetics may provide a faster route of informational transmission across generations and is becoming better understood via the molecular processes that are implicated in this phenomenon (e.g., methylation, histone modification, and non-coding ribonucleic acid (RNA) gene silencing; Jablonka and Raz, 2009). The idea that we are no longer investigating these issues of how organisms respond to change under the Darwinian “all or nothing” concept of adaptation, is exciting. Future studies assessing the interactions between developmental and transgenerational plasticity with epigenetic signatures and adaptation will be imperative for understanding how coral reef fishes and the ecosystems they support fare in the Anthropocene.

6 Knowledge gaps, technological advancements, and future directions

While experimental studies assessing how coral reef fishes respond to the stressors discussed here have rapidly expanded and produced a wealth of empirical data, especially since the start of the 21st century, knowledge gaps remain. Most notably, and because of the dynamic and multi-stressor nature of both local and global climate change, interactions between stressors are still challenging to anticipate. Such challenges preclude our capacity to predict species, population, and ecosystem health in the Anthropocene. However, technological advances (e.g., the National Sea Simulator at the Australian Institute of Marine Sciences, which allows for an array of stressors to be simulated in static or cycling conditions (e.g., Jarrold and Munday, 2018a, 2018b) over relevant time courses, and the array of innovations in genomics) will allow for multi-stressor, multi-level experimentation to not only be possible, but also time- and cost-effective. It is also important to recognize short-term and long-term variabilities in many of the discussed stressors. Different species may be sensitive to stressors over different timescales. Cycling of various stressors, especially in combination, has not always been possible under laboratory experimentation, but is an important next step. For example, studies revealed differential responses in the exercise physiology of coral reef fishes exposed to elevated, yet cycling $p\mathrm{CO}_2$ conditions (i.e., to more closely represent natural reef conditions; Hannan et al., 2020a) when compared to stable, yet elevated $p\mathrm{CO}_2$ conditions (Hannan et al., 2020b, 2020c). Moreover, individual experiments do not precisely predict the fate of future populations of coral reef fishes, but as we accumulate more empirical evidence, we can more robustly estimate species reaction norms and thus have better information for trait-based modeling. However, as demonstrated, studies addressing physiological effects of multiple stressors on coral reef fishes tend to take mechanistic approaches; yet experimental designs will need to grow in size and complexity to be more effective. Moreover, molecular underpinnings will need to be integrated more frequently into these studies, and such approaches are far more tenable today than before with ongoing advances in genomics (e.g., Bernal et al., 2020; Kang et al., 2022; Schunter et al., 2021). Data—and long-term datasets that *can* and *should be* accessed—can then be used to parameterize, test, and refine models to predict how combined stressors will affect coral reef ecosystems and biodiversity.

Mesocosm experiments and other approaches where laboratory studies are paired with field behaviors and responses (Cortese, 2021; Norin, 2018) can expedite understanding the consequences of anthropogenic stressors across the levels of biological organization, spanning from species to community structure and ecosystem function (Fordham, 2015). When physiological (e.g., as outlined and discussed in the above sections) and traditional ecological (e.g., collections, surveys, monitoring, and translocation) approaches are combined, studies can effectively start to bridge findings from the sometimes single-stressor conditions in the laboratory to the natural world. A mesocosm experiment, for example, is beneficial because it allows for replicated experimental designs (e.g., statistical power) and standardized physiochemical conditions, thus revealing elements observable in the wild (e.g., multi-species interactions, community structure, diversity, trophic complexity, nutrient cycling, etc.). Such combined eco-physiological studies can help identify where plasticity in certain physiological traits could aid resilience to climate change, for example (Seebacher et al., 2015). Mesocosm approaches can also reflect the consequences of sublethal and delayed effects on abundance and community structure, and identify feedback loops, species interactions, conditions that might drive species to endangerment, and the potential for restoration programs. Ultimately, maintaining the fine-scale resolution typically associated with physiological approaches while incorporating larger scale, more bio-complex aspects of an ecosystem via mesocosm experimentation will also help improve the accuracy of predictive models.

The variation in responses between individuals is also often overlooked in studies investigating the effects of various abiotic and biotic stressors on multiple traits and/or levels of organization (Sunday et al., 2014). Many overarching predictions are based on the average response of a population, which can often mask the—sometimes extreme—variability in how individuals respond. Identifying "winners and losers" and determining species' capacity for adaptation in the face of global change is crucial, but, especially in the case of "winners," can be detrimental, however, to abatement strategies (i.e., giving a false sense that species will thrive despite adverse conditions). Basic information on acclimation capacity as well as genetic (and epigenetic) variation in fitness-associated traits also aids in making more informed decisions about the impacts of various stressors on coral reef fishes over the timeframes that their habitats are changing. However, modern molecular methods—high throughput sequencing, the -omics (transcriptomics, genomics, metabolomics, proteomics), bioinformatics—paired with physiological approaches, elucidates the mechanistic basis for this crucial within and between generation plasticity.

It is also critical to understand how selection acts on variations in traits and heritability to better predict the fate of coral reef fishes in a multi-stressor world. This has been well studied with respect to fitness-related traits that are influenced by elevated temperatures (Rummer and Munday, 2017) and CO_2 (Munday et al., 2019), but only in a few select species and not in combination or with any other stressor. While the importance of investigating multiple traits simultaneously was highlighted earlier in this chapter, here within the context of selection, it is especially important. For example, if two traits are positively correlated, then selection can act unimpeded on the population by acting in the same direction as the most variation in the population (Munday et al., 2013). However, if two traits are negatively correlated, then selection may act orthogonally in the direction of the most variation in the population, which may result in limited influence on a population. Therefore, selection for one trait will decrease performance in the other and vice versa (Sunday et al., 2014). Describing this relationship between traits can therefore aid in predicting whether selection can act freely on a population, or will be constrained, thus limiting species' ability to adapt to future conditions. Identifying correlations among key traits is, indeed, an important step in predicting species persistence (Munday et al., 2019; Sunday et al., 2014). Incorporating evolutionary and environmental parameters, such as sensitivity analyses and evolutionary rescue models that have perhaps been more traditionally associated with terrestrial species and populations, may aid in predicting how coral reef fish populations will respond to an array of stressors in the Anthropocene.

7 Conservation and the future of coral reef fishes in the Anthropocene

Unequivocally, coral reef fishes, the ecosystems they support, and the services they provide are facing unprecedented threats from a wide range of multiple stressors, including global climate change. Coral reefs have the highest biodiversity in the marine realm and accommodate ~5000 fish species (Bellwood et al., 2012). Yet, the capacity of coral reefs to provide ecosystem services such as food and jobs, relied upon by millions of people worldwide, has declined by half since the 1950s (Eddy et al., 2021). Indeed, the rate at which conditions on coral reefs are changing today, since pre-Industrial times, as well as the increased frequency and severity of extreme environmental events (e.g., MHWs) is staggering. Since 2016, only 2% of the 2300 km-long GBR has not succumb to ocean warming induced coral bleaching (Hughes et al., 2021). These conditions keep coral reef fishes at a heightened risk when it comes to climate change and other anthropogenic influences, especially when other stressors are considered. Even worse, due to such high habitat specialization, coral reef fishes in biodiversity hotspots (e.g., Coral Triangle) are at an even greater risk of local extinction than regions with lower species richness (Holbrook et al., 2015).

In this chapter, we highlight that a mechanistic understanding of physiological processes governing individual organismal performance is the first step for identifying drivers of coral reef fish health and population dynamics in a multi-stressor world (Illing and Rummer, 2017). The array of physiological approaches we outlined in this chapter, in conjunction with new and emerging technologies, will help to reveal potential cause-and-effect relationships and enable scientists to advise conservation managers by scaling results from molecular, cellular, and individual organismal up to population levels (Illing and Rummer, 2017). In a perfect world, most of the anthropogenic stressors that coral reef fishes face today can and will be mitigated and hopefully quickly. However, it is more realistic that the coral reef fishes of the Anthropocene will continue to face new and emerging stressors. Now, more than ever, the future of coral reef fishes and the ecosystems they support depend on a diverse, passionate, and engaged interdisciplinary scientific community, knowledge co-production, evidence-based decision making, and the most innovative management and conservation strategies. In the spirit of conservation physiology and the quest for a "good Anthropocene" (Madliger et al., 2017), the coral reef fishes represent a great flagship for public engagement in the climate change crisis and an umbrella for the conservation of marine biodiversity in a rapidly changing future (Jepson and Barua, 2015).

Acknowledgments

The authors thank Erin Walsh for support with figure illustrations and Lisa Louth and Luen Warneke for assistance with references and formatting. Funding to J.L.R. is from the Australian Research Council Centre of Excellence for Coral Reef Studies and College of Science and Engineering at James Cook University. B.I. was funded by a postdoctoral fellowship from the German Research Foundation (BI 220/3-1). The authors would like to thank Bridie J.M. Allan, Jacey van Wert, and two anonymous reviewers for their constructive comments and suggestions on the chapter.

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