

Review

Recent Advances in Understanding the Effects of Climate Change on Coral Reefs

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Abstract: Climate change is one of the greatest threats to the persistence of coral reefs. Sustained and ongoing increases in ocean temperatures and acidification are altering the structure and function of reefs globally. Here, we summarise recent advances in our understanding of the effects of climate change on scleractinian corals and reef fish. Although there is considerable among-species variability in responses to increasing temperature and seawater chemistry, changing temperature regimes are likely to have the greatest influence on the structure of coral and fish assemblages, at least over short–medium timeframes. Recent evidence of increases in coral bleaching thresholds, local genetic adaptation and inheritance of heat tolerance suggest that coral populations may have some capacity to respond to warming, although the extent to which these changes can keep pace with changing environmental conditions is unknown. For coral reef fishes, current evidence indicates increasing seawater temperature will be a major determinant of future assemblages, through both habitat degradation and direct effects on physiology and behaviour. The effects of climate change are, however, being compounded by a range of anthropogenic disturbances, which may undermine the capacity of coral reef organisms to acclimate and/or adapt to specific changes in environmental conditions.

Keywords: adaptation; acclimatization; thermal bleaching; ocean acidification; novel ecosystem; distorted food webs

1. Introduction

Climate change is having profound effects on the structure and functioning of ecosystems worldwide, with increasing temperatures and changes in physiochemical characteristics leading to shifts in taxonomic and functional composition, habitat degradation and loss, as well as declines in biodiversity and productivity [1]. The effects of climate change are most pronounced in tropical marine ecosystems (e.g., coral reefs) [2,3], because many tropical marine species often have narrow thermal tolerances and live at or near their upper thermal limits (e.g., [4]). On coral reefs, the major

habitat forming organisms (scleractinian corals) operate so close to their upper thermal limit that slight increases (≥ 1 °C) in temperature can cause large-scale mortality and habitat degradation [5]. Although coral reefs have been exposed to changing climatic conditions repeatedly over geological time [6,7], leading to the slowing or cessation of reef development, current environmental conditions and rates of change appear to be beyond those experienced in the past [8].

Research into the effects of climate change on coral reefs was initially focused on the thermal sensitivities of corals (e.g., [5,9]) and the effects of acute broad-scale coral loss on reef-associated organisms [10,11]. More recently, there has been an increasing emphasis on: (i) understanding the independent and interactive effects of ocean warming *versus* ocean acidification (oceanic uptake of rising atmospheric CO₂) [12]; (ii) the capacity of habitat-forming corals and reef-associated fishes to acclimatise and/or adapt to changing environmental conditions; and (iii) directional shifts in the structure of reef communities and associated ecological feedbacks. The purpose of this review is to summarise recent advances in our understanding of the effects of climate change on coral reefs, focusing on taxa that have received the most attention in the literature; scleractinian corals and teleost fish.

2. Reef-Building Corals

2.1. Effects of Increasing Temperature

The most conspicuous effect of climate change on coral reefs thus far, has been so called “mass-bleaching” of scleractinian corals [3,13,14], which occurs when temperatures exceed the physiological tolerances of a large number of different coral species. Thermal stress causes widespread declines in the abundance of symbiotic zooxanthellae and their photosynthetic pigments, which are the primary source of nutrition for most corals. While bleached corals can recover following moderate or short-term exposure to adverse environmental conditions, there have been some recent episodes of extremely severe and widespread bleaching that resulted in extensive coral mortality (e.g., [14]), generating considerable concern about the fate of corals and coral reefs (e.g., [3,15]). In 1998, severe bleaching killed up to 90% of corals across much of the Indian Ocean, and environmental conditions that caused this extensive coral loss are expected to recur almost annually within coming decades [14,16,17]. Depending on the rate and magnitude of ongoing increases in ocean temperatures, coral-dominated habitats could become dominated by fleshy seaweeds, or at the very least, become drastically altered in terms of coral composition ([2,18], Table S1).

Projected climate change and associated increases in the incidence of mass coral bleaching have led to dire predictions of wholesale coral loss, even as early as 2050 (e.g., [3,14]). However, bleaching susceptibility varies greatly within and among coral taxa (e.g., [19,20]), suggesting there will be marked changes in the structure of coral assemblages (e.g., [21]) rather than simultaneous and comprehensive loss of scleractinian corals. There has been extensive research into bleaching susceptibility, mostly comparing the proportion of colonies from different coral genera that bleach during a distinct bleaching event. However, these data are almost universally based on studies at just one location (e.g., [9]) and there have been very limited comparisons among locations (see [22]). A meta-analysis of data from 68 different studies that document bleaching events in the Indo-Pacific (spanning Kenya to Panama), reveal the mean percentage of colonies that bleached ranges from 85.3% for *Seriatopora* down to <1.0% for *Heliofungia* (Figure 1). Given disproportionate effects on certain corals, ocean warming and bleaching are likely to lead to shifts in coral composition (see also [23]). However, increasing incidence of coral bleaching will not necessarily favour those corals that have highest resistance to ocean warming and bleaching [13,24]. Importantly, coral genera that exhibit highest rates of bleaching (e.g., *Seriatopora*, *Stylophora*, *Acropora*) are often capable of relatively rapid recovery in the aftermath of acute disturbances (e.g., [25]), owing to high rates of growth and recruitment. The extent to which bleaching-resistant *versus* weedy corals come to dominate coral assemblages will depend on the frequency *versus* severity of future mass-bleaching episodes (e.g., [26]). Frequent bleaching episodes are

likely to suppress abundance of those corals that are the first and worst affected (e.g., *Acropora*, [22,27]), whereas infrequent but severe bleaching episodes will likely favor those corals that can recover rapidly in the aftermath of such disturbances [24,25].

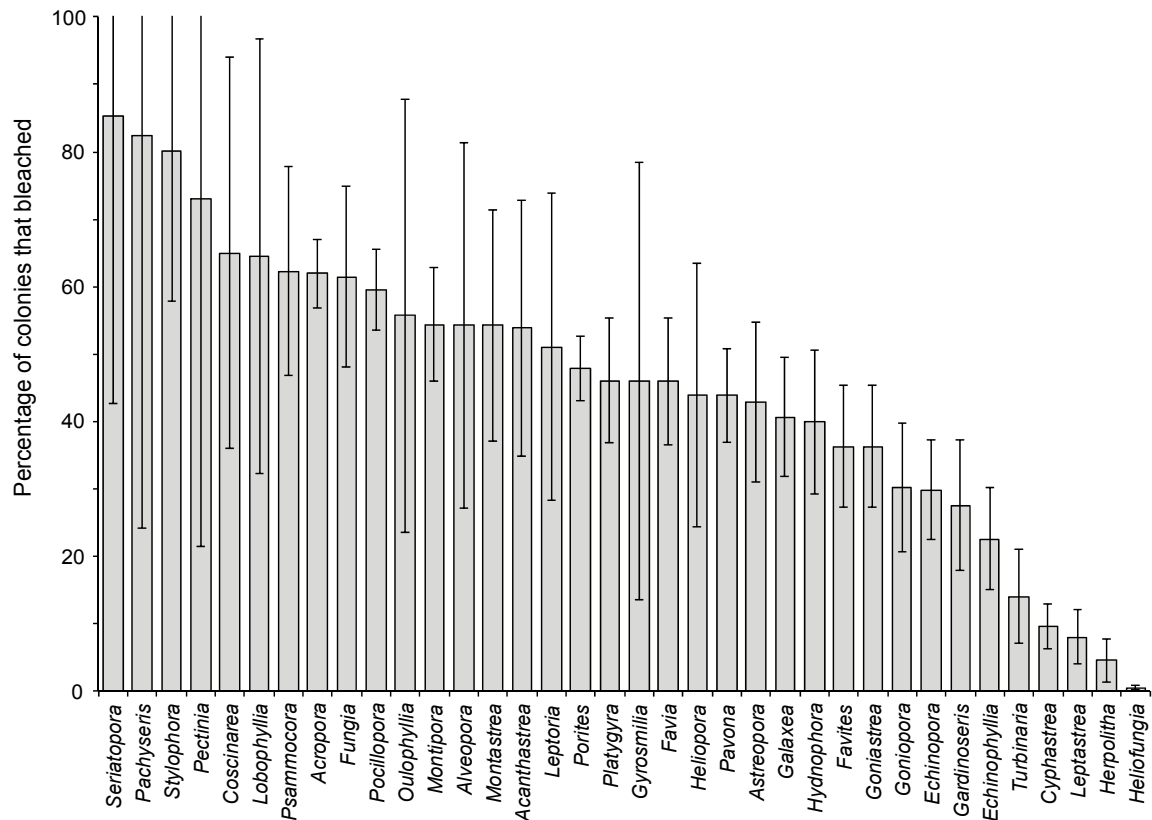


Figure 1. Taxonomic variation in bleaching susceptibility among 36 Indo-Pacific coral genera. Data presented is the percentage of coral colonies that exhibit bleaching, averaged across 68 studies conducted between 1982 and 2005, and spanning from Kenya to Panama (see [28] for specific details). Standard error bars indicate variation among 4–148 studies for each genus.

While extreme increases in ocean temperatures may cause extensive bleaching and mortality of corals (e.g., [13]), even moderate increases in temperature may have important demographic consequences for corals, moderating growth (e.g., [29]) and/or reproduction (e.g., [30]). The general relationship between an organism's performance (e.g., growth and reproduction) and temperature is a hump-shaped curve, where moderate increases in temperature can have potentially beneficial effects on performance (Figure 2). However, exposure to ever increasing temperatures will ultimately lead to marked declines in organism performance (e.g., [29]), culminating in high levels of physiological stress (e.g., bleaching for corals) and mortality. On Australia's Great Barrier Reef, there is recent evidence that growth rates of massive *Porites* have declined substantially since 1990 [31], which may be due to chronic increases in ocean temperatures and/or periodic cessation of growth following increasingly frequent and severe positive temperature anomalies and bleaching episodes [32]. Similarly, Cantin *et al.* [16] showed that growth rates of the robust coral, *Diploastrea heliophora* have declined by 30% since 1998 in the Red Sea (see also [33,34]). However, other studies (e.g., [35]) have revealed positive effects of increasing temperature on coral growth, mostly at high-latitude locations [36]. Declines in coral growth will impact directly on the resilience of corals to ongoing environmental change and disturbances, and also contribute greatly to sustained declines in cover of live corals [37].

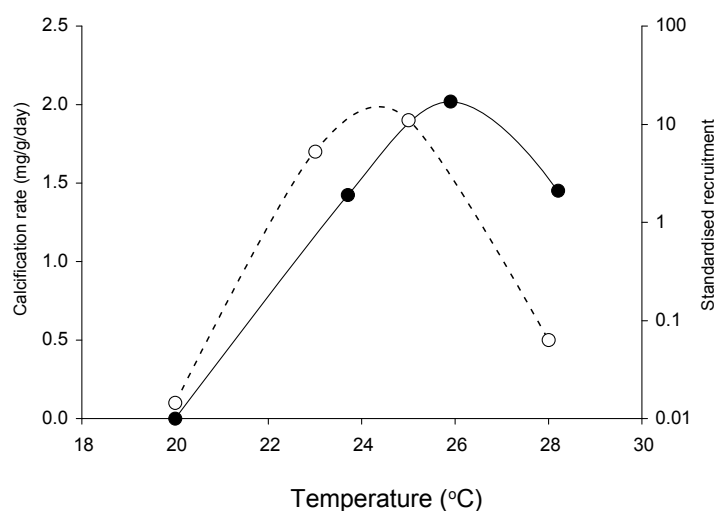


Figure 2. Temperature performance curves for *Pocillopora damicornis* from Hawaii showing changes in calcification (open circles), following Jokiel and Coles [29] and standardised recruitment rates (grey circles), following Jokiel and Guinther [30] when corals are exposed to increasing temperature within experimental settings. Both growth and reproduction were optimal at ~26 °C, which corresponds with the normal summertime temperature to which these corals were naturally exposed [29].

2.2. Effects of Ocean Acidification

Coral reefs are reported to be among the most sensitive ecosystems to the ongoing effects of global climate change [38], not only because reef-building corals bleach, and often die, following even moderate increases in ocean temperatures, but because scleractinian corals are expected to be extremely sensitive to sustained and ongoing changes in seawater chemistry [3]. Changes in seawater chemistry (specifically, declines in pH and reduced availability of carbonate ions) are directly attributable to increases in atmospheric CO₂ concentrations, and corresponding increases in the amount of anthropogenic CO₂ dissolved in the oceans [39]. Experimental studies generally show that projected changes in seawater chemistry will compromise calcification rates of reef-building corals (e.g., [6,40–42]), but it is clear that effects of ocean acidification, like ocean warming, will vary both spatially and taxonomically. Notably, the locations that are least affected by ocean warming (e.g., high-latitude reefs) are likely to be the first and worst affected by declining aragonite saturation [36]. Ocean acidification also appears to exacerbate sensitivity of corals to increasing temperatures [43], resulting in higher severity of bleaching for a given increase in temperature. In microcosm experiments, Dove *et al.* [44] showed that many corals (*Acropora*, *Seriatopora*, *Montipora* and *Stylophora*) could not withstand the combination of elevated temperature and reduced aragonite saturation expected to occur on reefs by 2050, while some corals (e.g., *Goniopora*) did survive even though they bleached during warmer months.

Considerable research is still required to establish which corals will be “winners” and “losers” under changing climatic conditions (e.g., [45]) especially when it comes to considering the simultaneous effects of ocean warming and acidification. There is currently very limited data with which to assess which corals are more or less resilient to ocean acidification (but see [44]), though it does seem that changing temperature regimes (cf. changes in seawater chemistry) are going to have the greatest influence on the structure of local coral assemblages, at least in the short to medium term. Notably, there is increasing evidence that corals can effectively and efficiently regulate their internal pH [46] and thereby, mitigate the effects of ocean acidification [47]. Increasing physiological costs of pH regulation may lead to further declines in coral growth and reproduction [3], though the energetic impost may be minimal [46].

2.3. Acclimatisation and Adaptation of Reef-Building Corals

Direct negative effects of climate change will continue to be experienced by corals in the near future. However, available evidence indicates that at least some species and populations have the capacity to acclimatise and/or adapt to warmer and more acidic conditions (Table S1f). Several coral species already persist in environments with similar conditions to those expected at the end of the century. Corals withstand 34–35 °C summers in the Persian Gulf, exhibiting bleaching thresholds that are ≥ 2 °C higher than coral reefs elsewhere in the world [48]. Additionally, recent studies show that corals maintain calcification rates under low aragonite saturation states ($\Omega_{ar} < 1.0$ –2.5) at naturally acidified locations in the Indo-Pacific and Caribbean [49–51]. Notably, only a hardy subset of regional diversity is typically represented at these sites ([49,50,52] but see [53]) indicating that the scope to withstand future climate conditions is inherently variable among species and populations [20,44]. A caveat of this interpretation is the potential mismatch between historical and contemporary rates of environmental change and evolution [54]. However, repeated thermal stress events over the past two decades provide new evidence that coral bleaching thresholds can increase over relatively short timescales. Some of the genera that suffered the most severe bleaching in the 1990s, including *Acropora*, *Montipora*, *Stylophora* and *Pocillopora* have exhibited increased resistance to bleaching in the 2000s on the Great Barrier Reef [55,56], Southeast Asia [57], Moorea [58], and the Maldives [59]. Follow-up species-specific investigations are required to determine whether these increases in bleaching resistance are due to acclimatisation of corals that recovered from initial bleaching [60], selection for heat-resistant genotypes/epigenotypes (*i.e.*, adaptation) [61], or a combination of these processes.

Interactions between multiple symbiotic partners shape the health, tolerance limits, and phenotypic plasticity of the coral holobiont [62,63]. The scope for the coral host and their complement of *Symbiodinium* to respond to environmental change is outlined herein, although other microbial partners may also be important for coral evolution [64]. Coral hosts contribute to the stress tolerance of the symbiosis through the regulation of photoprotective and antioxidant systems [64,65], increased heterotrophy [66], and potentially also symbiont cell densities [67]. Corals living in exceptionally warm locations have been recently shown to exhibit higher levels of expression of candidate genes involved in stress resistance traits compared with conspecifics in cooler environments [68–71]. For example, *Acropora hyacinthus* colonies living in a fluctuating thermal environment show elevated baseline expression of multiple genes including heat shock proteins and antioxidants, which likely enables an efficient response to regular pulses of temperature rise [68]. A proportion of these expression signatures is inducible by experience of warming, yet a remainder show fixed differences between populations, indicative of local adaptation [71–74]. For instance, positive host-driven acclimatisation has been observed over days to years of exposure to warming [60,71,73,74]. For instance, Ainsworth *et al.* [74] recently showed that subjecting corals to sub-bleaching temperatures stress before reaching critical bleaching temperatures decreased host cell mortality and *Symbiodinium* loss in *Acropora aspera*. If bleaching thresholds remain unchanged, the authors predicted that such an acclimatory mechanism would be lost with future warming. Ultimately, the extent of acclimatisation remains constrained by the genotypes of symbiont partners [71,75]. In the coral host, evidence for local adaptation to temperature is further supported by genetic differences between conspecific corals living in warm *versus* cool habitats in the absence of dispersal barriers (e.g., neighbouring back reef pools) [76]. Heat stress experiments on the offspring of several corals including species of *Acropora*, *Goniastrea*, *Platygyra* and *Porites* confirm that local and regional variation in heat tolerance is passed onto offspring [69,77–80]. Inheritance has been primarily attributed to genetic effects, [69,77,81], however epigenetic and maternal processes (forms of transgenerational acclimatisation) are also likely to influence the phenotype of host offspring [82]. Despite the examples provided, demographics of coral host populations including declining effective population sizes and relatively long generation times (first sexual reproduction at ~4–8 years) [83,84] suggest that they may not be able to keep pace with contemporary warming [17,85]. However, information is currently lacking on other features of

adaptive capacity including standing heritable variation for heat tolerance (but see [77,81,85]) and the prevalence of somatic mutations, interspecific hybrids, and epigenetic modifications as sources of novel variation under selection [61,86–88].

Corals can also achieve large gains in their thermal tolerance over short timescales by forming associations with heat tolerant *Symbiodinium*. Types (or “species”) of *Symbiodinium* vary widely in their capacity to prevent and repair photosynthetic damage, which is a major source of oxidative stress in the coral host [89–93]. Several (but not all) corals are able to take advantage of this diversity at symbiosis establishment, either through non-specific uptake of *Symbiodinium* from the environment during early life-history [94] or maternal provisioning of multiple *Symbiodinium* genotypes [95]. Acute or chronic changes in temperature can cause shifts in the relative abundance of *Symbiodinium* types within the host [96–100]. Classic examples are the greater prevalence of heat tolerant *Symbiodinium* D1 (*S. trenchi*) [101] in several bleaching resistant or warm-water symbioses around the world (e.g., [102–105]). However, heat tolerance has evolved across *Symbiodinium* lineages [90], and recent studies have shown that members of C1 [106,107] and C3 (*S. thermophilum*) [80,108] also exhibit exceptional heat tolerance in particular hosts and regions. Further characterisation of novel *Symbiodinium* types (e.g., [100]) and their physiology is expected to identify additional stress tolerant combinations. For *Symbiodinium* types to continue to maintain functional mutualisms with their coral hosts, they will themselves need to adapt to warming. Traits of *Symbiodinium* populations including their large size ($>10^8$ per adult host), fast asexual turnover (days to weeks), and cryptic sexual recombination are expected to maintain and generate high numbers of mutations upon which selection can potentially act [88,109–111], and researchers are currently working towards quantifying adaptation rates in these important symbionts.

In comparison to temperature, relatively little is known about potential mechanisms involved in maintaining net calcification under reduced aragonite saturation arising from increases in $p\text{CO}_2$. Inter-species variation in physiological performance under elevated $p\text{CO}_2$ generally favouring poritids over acroporids and pocilloporids (e.g., [42,112–114]) has been linked to differential capacity to acclimatise via internal regulation of pH at the site of calcification [46]. Additionally, single species have been shown to be able to acclimatise to changes in $p\text{CO}_2$ over days to weeks by recovering their respiration rate (*Pocillopora damicornis*) [82] or stabilising the expression of candidate genes involved in metabolism and skeletal deposition (*Acropora millepora*) [115]. As with temperature, there is some capacity to mediate energetic effects of acidification through increased heterotrophy [116], but there is no evidence (from limited data) to suggest that corals will associate with novel *Symbiodinium* partners that differ in performance under elevated $p\text{CO}_2$ [117,118]. While initial research has investigated transgenerational acclimatisation to combined acidification and temperature stress [82], further work is required to disentangle positive and negative effects on offspring. At present, virtually no studies have explored intra-species and -population variation in tolerance to elevated $p\text{CO}_2$ (but see [42]) and whether such variation has a heritable genetic basis (e.g., [119]). Yet, this information is critical in advancing understanding of the potential of $p\text{CO}_2$ sensitive species to persist under future acidification.

3. Reef Fishes

3.1. Direct Effects

While reef fishes will be widely affected by climate-induced changes in habitat composition and structure (discussed below), ocean warming and acidification will also have substantive direct effects on physiology, behaviour, abundance, distribution, and composition of reef fishes. Being ectotherms, the metabolic rates and energy requirement of reef fish are largely dictated by local water temperature [4,120], such that increasing temperatures will increase the rate of biochemical and cellular processes, and hence the energetic cost of activity, growth and reproduction [120]. Similarly, ocean acidification is predicted to be energetically costly for reef fishes because they depend on a tightly regulated plasma $p\text{CO}_2$ to facilitate oxygen binding and transport to tissues and organs. They regulate their internal

acid-base balance, primarily through the differential excretion of H^+ and HCO_3^- ions which becomes increasingly more difficult against an acidic gradient [121].

The energetic cost imposed by exposing fishes to increased temperatures is most apparent by quantifying changes in metabolic rate and aerobic scope [4]. Numerous studies have reported 30%–40% increases in basal metabolic energy requirements and substantive reductions in aerobic scope of coral reef fishes at temperatures 2–3 °C above current summer maxima (e.g., [122–126], Table S2), which is necessary for demanding physiological activities. Concurrent increases in energetic requirements and reduced physiological capacity, suggest that any increases in temperature are likely to negatively impact these species. Although energy requirements increase quickly with rising temperatures (e.g., [127,128]), the direct implications of reduced aerobic scope on a species fitness and ecology are unclear [129] largely because fishes can differentially allocate energy to growth, reproduction or activity. Notwithstanding these uncertainties, aerobic scope has been related to swimming performance [125], hypoxia tolerance [130] and competitive dominance [131] in some coral reef fishes. Johansen and Jones [125] showed that following a 3 °C increase in water temperature several species of damselfish were no longer able to swim against the currents commonly encountered in their respective coral reef habitats. Similarly, reductions in hypoxia tolerance under elevated temperatures could force some species to abandon shelters where oxygen levels frequently get depleted at night, such as within the branches of coral colonies, and move to more open habitats with greater risk of predation [130] or even relocate to cooler more oxygen rich waters [132,133].

A temperature-induced 30%–40% rise in energy demands and/or oxygen consumption is likely to have direct implications for the viability of populations as available energy is directed away from growth and reproduction and toward basal metabolic maintenance. Although enhanced larval growth and settlement success has been linked to small temperature increases within the natural range (e.g., [134,135]), recent experimental studies have shown that 1–3 °C increases in water temperature led to marked reductions in somatic growth of both larval and adult coral reef fishes [136,137]. These declines in growth were evident even when food supplies were increased [136,137] suggesting there is limited capacity to compensate for the increased energy demands through elevated food intake. Similar results have been found in the large predatory reef fish, *Plectropomus leopardus*, with significant reductions in activity, movement and growth under 3 °C temperature increases even when provided with unlimited food [128,138]. Such reductions in growth are likely to lead to increased larval duration and mortality rates, and reduced adult body size and productivity of reef fish populations under warming oceans [139,140], particularly in large reef fishes which are likely to be more sensitive to the expected temperature changes [141].

Available evidence also suggests that warming ocean temperatures will influence the reproductive behaviour of coral reef fishes. Water temperature is an important trigger for production of reproductive hormones, gonad development and spawning [142,143]. Elevated ocean temperatures, therefore, may be expected to lead to earlier onset and shorter breeding season/s in the tropics compared to longer breeding seasons at higher latitudes [144]. This potential effect on reproductive output is further offset by increased metabolic costs and reduced capacity for sustaining activity at elevated temperatures. Increases in water temperatures of 1.5–3.0 °C above current summer average on the Great Barrier Reef (28.5 °C) led to marked declines in egg, clutch, and offspring size in the spiny chromis, *Acanthochromis polyacanthus*, causing reduced reproductive output [136,145]. Although food availability moderated the effects of increased temperature on the number of breeding pairs, fishes on a high ration diet still produced fewer and smaller eggs, and smaller offspring [136].

In contrast to temperature, the effects of elevated CO_2 on the aerobic scope, growth and reproduction of coral reef fish are less certain. The energetic cost of acid-base regulation under elevated CO_2 is expected to affect respiration, circulation and metabolism of some fishes at extreme levels of environmental CO_2 (>10,000 μatm) [146]. Empirical evidence for the negative effects on metabolic performance at CO_2 concentrations predicted for the next century (up to 1000 μatm) are, however, variable. The aerobic scope and growth rate of reef fishes has been reported to decrease,

increase, or not change in response to elevated CO₂ (e.g., [122,147–149], Table S3). Further, elevated CO₂ stimulated breeding activity in an anemonefish, with the number of breeding pairs, clutches per pair, and eggs produced per clutch being greater in fishes held at high (1000 µatm) CO₂ compared to those at control (430 µatm) CO₂ [148,150].

The greatest effect of elevated CO₂ on reef fishes appears to be through altered behaviour and sensory impairment. The vast majority of research suggests that, in the absence of adaptation, near-future CO₂ levels (*ca.* 1000 µatm) will have a dramatic effect on the sensory abilities of reef fishes [151]. Numerous studies have reported acute exposure (mean = 7.46 days, range 4–28 days) to elevated CO₂ to disrupt olfactory systems of fishes, in particular their ability to detect and avoid predators (e.g., [152–155]), detect reefs and locate suitable settlement sites [147,153,156], and hence the replenishment of reef fish populations. Exposure to elevated CO₂ has also been shown to impair auditory [157] and visual systems [158], as well as general cognitive functions such as lateralisation, boldness, escape response, and learning [131,154,159,160]. Collectively, these effects have been shown to translate to a 5- to 9-fold increase in mortality for recently-settled damselfish exposed to elevated CO₂ and then released onto a reef [153,155]. Such an increase is critical given the already extremely high mortality of fishes immediately following settlement (e.g., [161,162]). The prevalence of disrupted function across multiple sensory systems suggests that elevated CO₂ affects central neural processing rather than individual sensory systems in isolation, and has been related to interference with a major neurotransmitter receptor, GABA-A [151,163].

3.2. Acclimation and Adaptation of Reef Fish

Short-term acute exposure to elevated temperatures and pCO₂ have marked effects on the fitness and performance of reef fishes, however the longer-term effects of climate change will depend upon the capacity of fishes to acclimate or adapt to changing conditions. While individual fishes appear to have limited capacity to acclimate to elevated temperature over several months [130,136], there is some evidence for localized adaptation in some traits of wild populations as well as experimental data suggesting developmental and transgenerational acclimation. Some wild-caught equatorial fish species have shown increased hypoxia tolerance befitting the greater severity and frequency of hypoxia in warmer regions [164]. Donelson *et al.* [123,124] demonstrated that rearing *A. polyacanthus* from hatching at elevated temperatures (+1.5–3.0 °C) reduced their resting metabolic rate, with aerobic scope seeming to be completely restored to control levels when both parents and offspring were reared under these conditions. Thermally acclimated fish were, however, smaller and in poorer condition than control fish [123,124], and only fishes reared at 1.5 °C showed any capacity for reproductive acclimation [145] suggesting physiological acclimation may come at a cost. Although this evidence for physiological adaptation in this small-bodied species with short generation time is promising, the potential for other species with larger body size and longer generational times to acclimate to elevated temperature at the predicted rate of global warming is largely unknown. Given their increased sensitivity many species may simply be forced to relocate to cooler regions with less severe hypoxic conditions [132] and less impact on reproductive capacity and timing [143,144].

The potential for fishes to acclimate to elevated CO₂ is variable and appears to be largely trait dependent. Elevated CO₂ reduced the growth and survival of juvenile anemonefish, however these effects were absent when the parents are also reared under elevated CO₂ [148]. In contrast, declines in the capacity of reef fishes to escape predators were not improved by transgenerational acclimation [160]. Similarly, fishes in naturally acidic waters surrounding CO₂ seeps in Papua New Guinea were found to display similar behavioural abnormalities and sensory impairment as those reported in acute experimental studies [165]. Although this may be taken as evidence for limited scope of sensory adaptation across generations it is likely confounded by the influx of individuals and genes from unaffected areas around the seeps. Despite the behavioural abnormalities and sensory impairment of the reef fishes tested from around the CO₂ seeps there were limited differences in the richness, composition and abundance of fish assemblages between the seeps and adjacent control areas [165].

Interestingly, several small prey fishes were more abundant around one of the seeps than control reefs, and it was hypothesized that this was related to differences in habitat between the seep and control reefs. Similarly, the negative effects of elevated CO₂ on the behavior and performance of temperate reef fish have been demonstrated to be dampened by habitat modification around CO₂ seeps [166].

Until now, there has not been any research explicitly focused on the adaptive capacity of fishes to cope with climate-induced shifts in habitat availability, but anecdotal evidence suggests that any changes in patterns of habitat-use, if apparent, are likely to negatively impact on affected populations. For highly specialised species, patterns of resource use appear insensitive to geographic variation in resource availability [167], suggesting that there will be limited capacity for temporal shifts in habitat use. Even for species with flexible patterns of habitat use, preferred habitats often provide significant fitness advantages [168], and so populations that are restricted to suboptimal habitats are likely to have slower growth, reduced fecundity, or even lower survivorship. Novel ecosystems that arise due to fundamental shifts in habitat structure [169] are expected to support altogether different fish assemblages, dominated by habitat generalists or species with strong preferences for non-coral habitats. Influx of new species into established habitats have in the past resulted in strong dominance of single invasive species, similar to the lionfish explosion in the Caribbean [170], and similar scenarios may also unfold as tropical species start relocating into more subtropical and temperate regions [171,172].

3.3. Indirect Effects

Together with the effects on physiology and behaviour, climate induced changes to reef habitats are already having a marked effect on the structure and function of reef fish assemblages [169,173,174]. The increased frequency and/or severity of climate related disturbances, such as coral bleaching and storms, are leading to declines in live coral cover, reductions in structural complexity, changes in coral composition and greater habitat fragmentation [12,175,176]. Indeed, ongoing degradation of coral reef habitats is the most immediate pathway by which climate change will affect coral reef fishes [10,11]. While <12% of reef fishes are considered to be directly reliant on live coral [177,178], a far greater proportion of species (up to 75%, [179]) experience declines in abundance following extensive coral loss [169,180–184]. These declines likely reflect the reliance on live corals for food, refuge, settlement habitat, or the greater availability of prey in coral rich areas [178,185].

Positive relationships between live coral cover and the abundance, biomass and/or diversity of reef fishes are widespread (e.g., [179,180,186]). There is, however, substantial variation in the reliance on live corals among fish species, from dietary and habitat specialists that are highly dependent on a single coral species [187,188] to species that show no apparent association with live corals as either juveniles or adults (e.g., [189]). Not surprisingly it is the obligate corallivores and habitat specialists that are the first to decline following widespread coral loss [10,11,190,191]. Reductions in the cover of live coral are often accompanied by reductions in the topographic complexity of reef habitats due to the dead coral skeletons being eroded by biological and physical forces [192–195]. It is this loss of the biological and physical structure provided by scleractinian corals, however, that appears to have the greatest impact on reef fish assemblages [196,197].

The structural complexity of reef habitats is a major determinant of reef fish abundance and diversity (e.g., [184,196–199]), with this relationship typically associated to the role of corals in creating complex three-dimensional habitats that increase habitat area and moderate biological interactions. Importantly, live corals provide relatively fine-scale complexity, creating microhabitats and refugia that mostly benefit small bodied and juvenile fishes [178,197,200]. As such, it has been hypothesised that larger bodied fishes are less sensitive than smaller bodied fishes to coral loss (e.g., [201]). However, a recent meta-analysis of >400 coral reef fish species revealed no relationship between fish body size and changes in abundance following coral loss, either with or without loss of structural complexity [173]. Although larger-bodied species with longer generation times may take longer to respond, reductions in reef complexity will negatively affect both large- and small-bodied fishes [184,202,203] and is predicted to reduce the productivity of coral reef fisheries [174,204,205].

Together with reductions in coral cover and complexity, changes in the condition and composition of coral assemblages are likely to have marked effects on reef fishes. Recently bleached corals (*i.e.*, with skeletons intact) have been shown to support fewer species and individuals due to reduced settlement of some fish species [206,207], increased predation [208], and/or greater competition [209]. The effect of bleached corals is likely to be short-lived, with corals either recovering or dying within days to weeks. Subsequent changes in habitat configuration are, however, likely to have lasting effects on fish communities. The differential loss of some species under global warming and ocean acidification will alter coral diversity and community composition, and may lead to “novel” configurations [39,45,169]. Many reef fish exhibit clear preferences for certain coral species (e.g., [178,210–212]) and highly specialised fish species are often disproportionately affected by coral depletion [213]. Different coral species and morphologies have been shown to support different fish assemblages (e.g., [199,214,215]) thus the taxonomic and functional composition of reef fishes will depend on the composition of future coral communities. In addition, the diversity of coral assemblages have been positively related to the species richness, and to a lesser extent the abundance, of fish assemblages in highly diverse systems [214,216]. Subsequently, reef fish assemblages in the most diverse systems may be the most vulnerable to changes in coral species composition and reductions in coral diversity, as these communities tend to contain a greater proportion of habitat and dietary specialists [217]. While the effects of reductions in fish species richness will be dependent on species identity, they are likely to negatively affect the productivity and function of reef fish communities [218,219].

3.4. Ecological Feedbacks

Reductions in coral cover are often accompanied by increases in abundance of other alternative habitat-forming organisms, such as macroalgae, that may further influence the behaviour, settlement, and survival of reef fishes. Indeed, a common response to loss of coral habitat is an increase in the abundance and/or biomass herbivorous fish species (e.g., [9,220,221]). Increases in herbivorous fishes following coral decline is partially dependent on recruitment of juvenile fish and therefore highly variable among species [11], and the increased availability of dietary sources. Increases in the abundance of grazing parrotfishes and surgeonfishes following coral loss have been reported to reflect changes in the availability of the epilithic algal matrix (EAM *sensu* [222]) the preferred feeding substratum for these fishes.

Herbivorous fishes have been shown to avoid areas of high macroalgal density, presumably in response to elevated predation risk [223]. Recent experimental work has suggested that recently-settled reef fish (15 spp) use olfactory cues to avoid macroalgal-dominated habitats [224]. Such avoidance is not, however, universal. Turf- and macro-algae that often dominate reefs following coral loss provide habitat for many species of juvenile fish, including herbivorous species of parrotfish, rabbitfish, and surgeonfish [225–229] and increased abundance of these juvenile fishes contributes to unique assemblages of herbivores on macroalgal dominated reefs [230,231]. Some recent studies have suggested grazing and browsing intensity on macroalgal-dominated reefs are broadly comparable to those on coral-dominated reefs [182,192,232], however there are few examples of herbivory being sufficient to reverse macroalgal-dominance and promote the recovery of corals (see [218,233] for exceptions). If rates of herbivory are high, the extensive removal of fleshy macroalgae will promote coral recovery, but will also lead to a loss of juvenile and adult habitat, and ultimately a decline in the abundance of herbivorous, and in particular browsing, fish [234]. Studies of recovering reefs in the Seychelles indicate that the capacity of browsing fishes to promote recovery is reliant on their biomass being >180 kg.ha [233], a value that is not commonly exceeded, even on relatively intact reefs with limited fishing pressure [234,235].

A reduction in coral cover also places greater predation pressure on remaining corals by resident corallivores. Obligate coral feeding butterflyfish can remove up to 3 g of coral tissue a day [236], and selective feeding on certain coral species may account for 50%–80% of their annual productivity [237]. On healthy reefs, where the cover of preferred corals is high, coral feeding by fish

may be of little consequence. However, high susceptibility of corals preferred by many coral feeders (e.g., *Acropora*, *Pocillopora*) to environmental stress means their occurrence will decline following disturbances and remaining colonies will come under increased grazing pressure.

4. Conclusions

Coral reefs are considered among the most vulnerable ecosystems to sustained and ongoing changes in environmental conditions due to climate change. Some corals do however, have exceptional capacity to withstand extreme temperatures, and fundamental shifts in environmental conditions are likely to exert strong selective pressure on contemporary populations and communities. The key issue however, is that coral reef ecosystems are being rapidly degraded not only due to climate change, but also more direct anthropogenic disturbances, which may undermine the capacity of corals and other reef-associated organisms to acclimate and/or adapt to specific changes in environmental conditions [17,238]. For coral reef fishes, climate change will have important indirect effects (due to coral loss and habitat degradation) as well direct effects on physiology, behaviour, abundance, distribution, and function. However, research has only just commenced to assess whether fishes may acclimatise or adapt to these changing environmental conditions. Important components of future research will be to test trans-generational acclimatisation and measure rates of contemporary adaptation to synergistic changes in biotic and abiotic conditions across a broad range of taxa, as well as the potential for species to behaviourally mitigate physiological limitations in performance.

Supplementary Materials: The following are available online at www.mdpi.com/1424-2818/8/2/12/s1, Table S1: Recently documented (last 5 years) effects of climate change on reef corals (a) declining coral cover; (b) reduced diversity and shifts in coral community composition; (c) declining or low rates of coral calcification; (d) favourable conditions for higher latitude corals; (e) recent adaptation and/or acclimatisation (<20 years); and (f) longer term adaptation and/or acclimatisation (unknown timescale); Table S2: Summary table of the effects of elevated seawater temperature on the activity, development, metabolism, reproduction, and sensory capabilities of coral reefs fishes. “+” indicates positive, “-” indicates negative, and “ns” no significant effect; Table S3: Summary table of the effects of ocean acidification on the activity, development, metabolism, reproduction, sensory capabilities, and survival of coral reefs fishes. Numbers in parentheses for control and treatment CO₂ are the pH of the seawater. “+” indicates positive, “-” indicates negative, and “ns” no significant effect. “*” denotes study was conducted around natural CO₂ seeps and as such an exposure time is not given.

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