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REVIEW

The effects of climate change on the ecology of fishes

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Abstract

Ocean warming and acidification are set to reshuffle life on Earth and alter ecological processes that underpin the biodiversity, health, productivity, and resilience of ecosystems. Fishes contribute significantly to marine, estuarine, and freshwater species diversity and the functioning of marine ecosystems, and are not immune to climate change impacts. Whilst considerable effort has been placed on studying the effects of climate change on fishes, much emphasis has been placed on their (eco)physiology and at the organismal level. Fishes are affected by climate change through impacts at various levels of biological organisation and through a large variety of traits, making it difficult to make generalisations regarding fish responses to climate change. Here, we briefly review the current state of knowledge of climate change effects on fishes across a wide range of subfields of fish ecology and evaluate these effects at various scales of biological organisation (from genes to ecosystems). We argue that a more holistic synthesis of the various interconnected subfields of fish ecology and integration of responses at different levels of biological organisation are needed for a better understanding of how fishes and their populations and communities might respond or adapt to the multi-stressor effects of climate change. We postulate that studies using natural analogues of climate change, meta-analyses, advanced integrative modelling approaches, and lessons learned from past extreme climate events could help reveal some general patterns of climate change impacts on fishes that are valuable for management and conservation approaches. Whilst these might not reveal many of the underlying mechanisms responsible for observed biodiversity and community change, their insights are useful to help create better climate adaptation strategies for their preservation in a rapidly changing ocean.

Introduction

Anthropogenic climate change is affecting a wide range of species and ecosystems across the globe [1]. Yet, our ability to accurately predict the structure and functioning of near-future biological communities and ecosystems in the Anthropocene remains limited. This is partly due to the diversity of individual species' responses linked to their different life histories, environmental tolerances, phenotypic plasticity, and scope for genetic adaptation. Furthermore, upscaling species-specific responses to climate stressors across higher levels of biological organisation (such as populations, communities, and ecosystems) has proven challenging [2]. This is partly due to the inherently complex intra- and interspecies ecological interactions that vary in space and time and are often difficult to quantify or forecast [3]. Interactive effects of multiple environmental stressors further complicate accurate predictions of future impacts, as they can have synergistic as well as antagonistic effects [4]. We urgently need to better understand and predict how global change will affect fish species at higher levels of biological organisation such as communities and ecosystems.

Bony and cartilaginous fish species span a total of $>$ 35,000 species globally [5], make up over half of all vertebrates on the planet, and perform key ecosystem functions, such as food production, maintenance of biodiversity, recycling and transport of nutrients, and sustaining ecosystem resilience [6]. They have a global distribution spanning from the equator to the poles, occur in the ocean as well as estuaries and freshwater systems, and can be found from intertidal habitats to the abyss. Fishes not only show strong responses to changes in their abiotic environment (e.g., salinity, pH, temperature, oxygen) [7], but also to their biotic environment [8]. The latter includes strong interactions with their habitat (especially for demersal species) and a wide range of positive and negative species interactions, such as competition, predation, grazing, parasitism, symbiosis, and disease. Their trophic interactions mediate energy flow within food webs and regulate biodiversity, productivity, and ecosystem stability [9]. Climate-driven alterations in fish communities and populations can thus have wide-reaching effects on the health and biodiversity of the ocean, on marine ecosystem functioning, as well as on humans through altered ecosystem services [10,11].

Predicting fish population and community responses to climate change requires a holistic consideration of the many processes and levels of biological organisation that regulate ecological interactions, behaviours, physiological performance, adaptive capacity, and fitness of fishes. Despite the breadth of the field of fish ecology, to date, we have predominantly gained insights into specific subfields of fish ecology, in particular warming effects on the physiology of individual fish species (Figs 1 and 2, S1 Table). Ocean acidification effects have also received considerable attention, although the empirical evidence for this stressor appears lower than that for warming effects (Fig 1A), even though this stressors is often considered in literature reviews (Fig 2A). The potential effects of hypoxia as a climate stressor on fishes remain severely understudied. Studies of climate impacts on fishes that link multiple climate stressors (e.g. warming, acidification, hypoxia and/or others), or that link multiple subfields of fish ecology (e.g. linking genetics, behaviour, physiology, community dynamics, and spatial ecology) are crucially lacking. These are important because fishes can acclimatise to changing abiotic conditions such as increased water temperature [12], compensate for biotic changes (e.g., ecological trade-offs) [13], move to escape unsuitable climates [14], alter gene expression associated with critical processes within generations [15], or genetically adapt across generations [16]. Moreover, most climate impact assessments on fishes have been performed at the organismal level, with still very little knowledge of climate effects on populations and communities (Figs 1B and 2B).

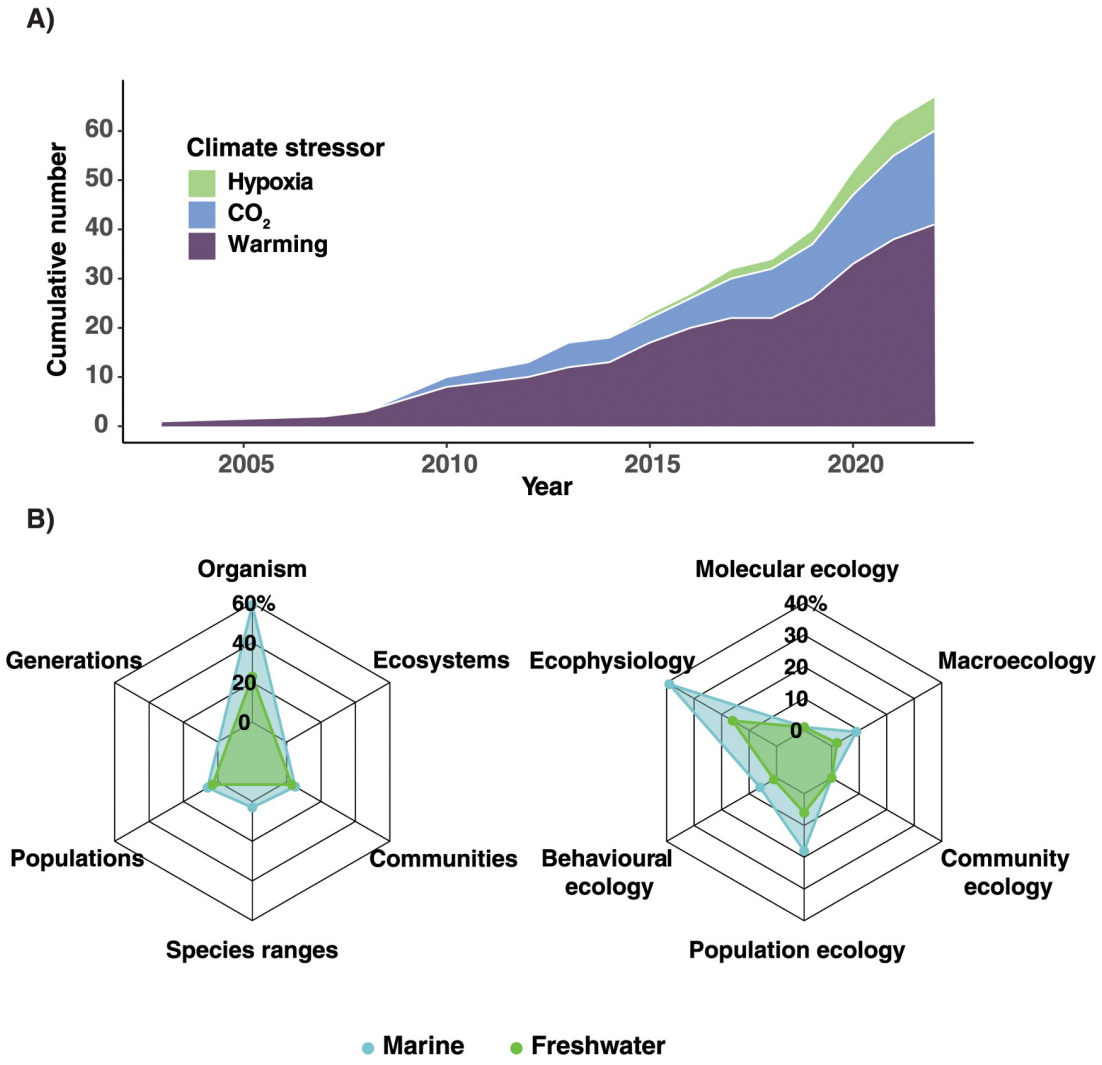


Fig 1. (A) Results from a quantitative literature review on published meta-analyses on the effects of climate change stressors on fishes. (A) Cumulative number of meta-analyses published over time, split for the various climate stressors. (B) Diagrams showing distribution of studies across different levels of biological organisation (left) and for the various subfields of fish ecology (right). See S1 Table for full details of the studies included.

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Here, we first briefly review the state of knowledge in terms of fish responses to key global climate change stressors (i.e., ocean warming, acidification, and to a lesser degree also hypoxia) and some of the key underlying mechanisms. We note that the majority of fish responses to climate change stressors have been tested under the worst-case climate scenario forecasts, that is, in the absence of significant greenhouse gas emission reductions (average temperature increases of ~ 2–4 ˚C above ambient, and average pH decreases of ~ 0.25–0.5 units below ambient [10,17,18]). Studies are urgently needed to test responses to less extreme climate change scenarios (i.e. reflective of greenhouse gas reduction scenarios; e.g. [19]). We still know relatively little about the levels of temperature or CO_2 increase at which various fish species start showing noticeable differences in their behaviour, physiology, ecology, etc. Negative effects on fishes can already be observed at pCO_2 increases of 100–150 μatm [20,21]. For

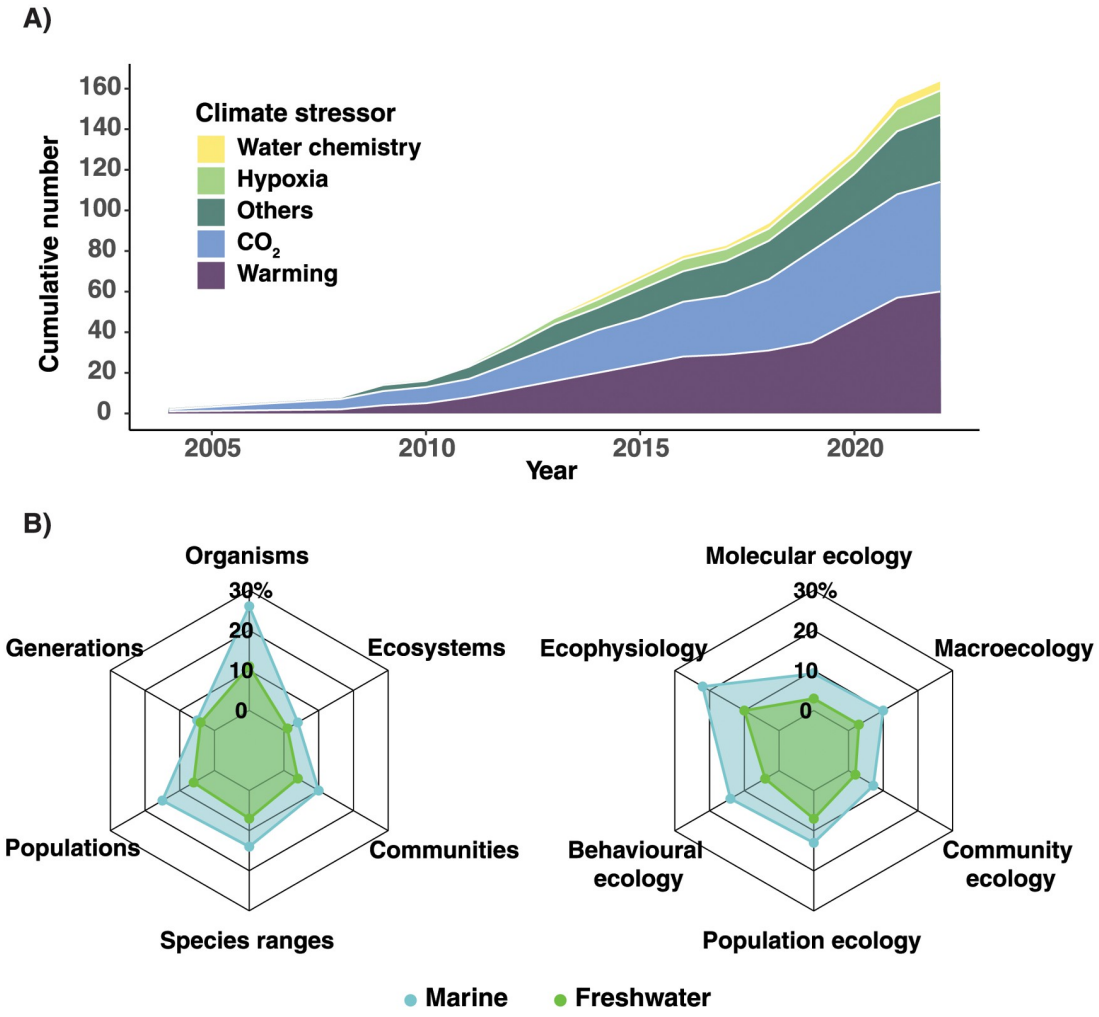


Fig 2. Results from a semi-quantitative literature review on published reviews and a quantitative literature review on systematic reviews on the effects of climate change stressors on fishes. (A) Cumulative number of reviews published over time, split for the various climate stressors. (B) Diagrams showing distribution of studies across different levels of biological organisation (left) and for the various subfields of fish ecology (right). See S1 Table for full details of the studies included.

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temperature, many fish species show elevated upper thermal tolerances (but not preferred temperatures) when slowly acclimated to increases of up to >25 ˚C [12], but exposure time and intensity of increase are important determinants and can inform us about responses to gradual climate warming vs extreme heatwave events [22]. However, fishes have a wide range of life history strategies that will result in considerable inter-species differences in responses to temperature and pCO_2 increases, which also depend on their life stage, if they live in the open ocean or coastal areas, and whether they are tropical/arctic (more sensitive) or temperature species.

We further assess climate change impacts at various levels of biological organisation (Fig 3) within the broader fields of molecular, organismal, population, community, landscape, ecosystem, macro-, fisheries, and conservation ecology of fishes, respectively. More extensive and detailed climate-related reviews and meta-analyses for specific subfields of fish ecology exist (S1 Table) but are not the focus of this review. Following the brief reviews of the various

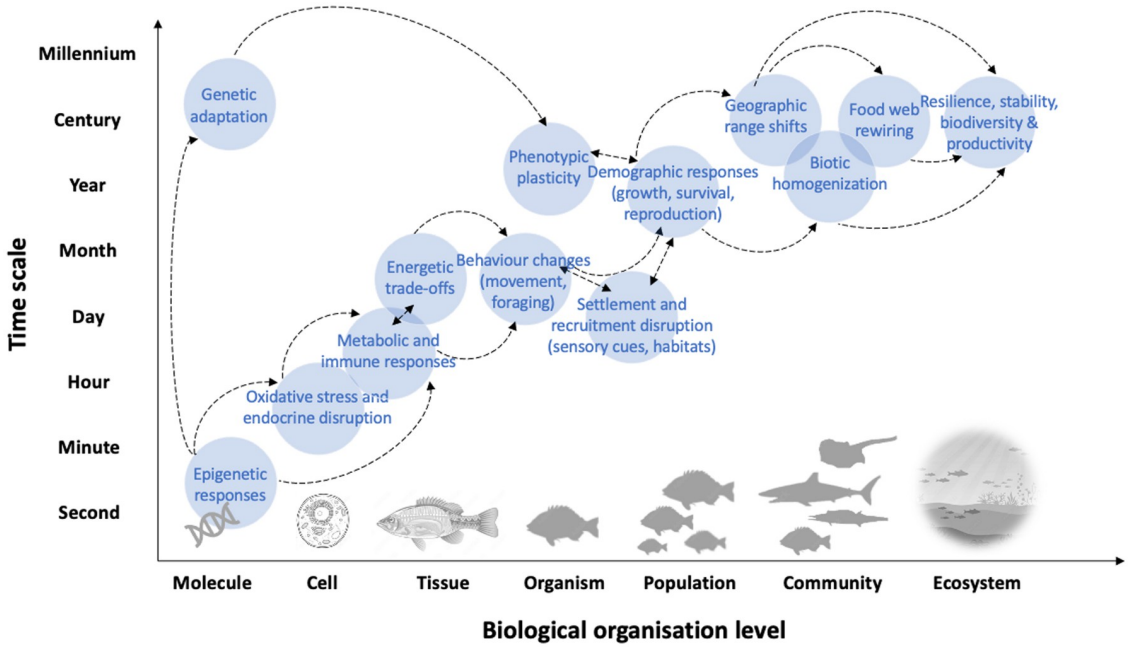


Fig 3. Conceptual diagram showing key processes that underpin the responses of fishes to climate change at different levels of biological organisation and response times. The graph highlights how the different levels and processes are potentially interconnected (arrows).

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subdisciplines of ecology, we then focus on the conceptual links across the different subfields of fish ecology and levels of biological organisation, because their synthesis is important for better understanding and predicting fish species responses to climate change from genes to ecosystems. As such, we discuss the relevance of natural analogues of climate change, meta-analyses, quantitative modelling, and paleobiology to help guide climate change research on upscaling fish responses to community- and ecosystem-levels, which could provide future projections that are relevant for fish management and conservation practices.

Molecular ecology

Molecular plasticity and (epi)genetic adaptation

This represents the lowest level of biological organisation at which fish responses to climate change stressors have been evaluated. It relates to changes at molecular levels, including alternation to the genome and altered expression of particular genes. Some ecophysiological responses also operate at cellular levels (e.g. neuro-endocrine functioning and changes to various types of cellular biomarkers), but these are discussed under 'Ecophysiology' below, where they are combined with ecophysiological alterations at the organismal level.

Recent advances in genomic and epigenomic techniques have started to reveal the genetic mechanisms underlying phenotypic plasticity and genetic adaptation of fishes in response to climate change [23]. Plasticity is often divided into responses that occur within an individual's lifetime (developmental and reversible) and across generations (parental effects and transgenerational plasticity) [24]. Aquarium-based manipulations have shown that some coral reef fish species such as such as damselfishes and clownfishes (Pomacentridae) are able to acclimate to higher ocean temperatures (1.5 and 3 ˚C warmer than current-day) within just one or a few

generations [25,26]. At the molecular level, this is driven by the increased expression of the metabolic pathway in the liver, which compensates for the impaired oxygen metabolism caused by higher temperatures [15,27–29]. Genome-wide epigenetic measurements have shown that impacts of thermal stress are passed from one generation to the next via loci-specific methylation changes, which can influence the expression of those metabolic pathways necessary to adjust aerobic scope under higher temperatures, such as is the case in the spiny chromis damselfish *Acanthochromis polyacanthus* [30,31]. Similar epigenetic responses have been documented in wild-caught fish species (Pomacentridae and Apogonidae) during marine heatwaves [32]. These studies provide support that some fish species might be able to adapt to ocean warming within just a few generations via epigenetic remodelling of their genomes. On the other hand, Wang et al. [33] showed that exposure of parent *Oryzias melastigma* to hypoxia resulted in negative impacts on reproduction in the next generations due to transgenerational and epigenetic effects.

Phenotypic plasticity and epigenetic adaptation might not be the only mechanisms that can help fish to cope with climate change. In coral reef fishes, natural populations have a standing genetic variation that can be advantageous when natural selection occurs under stressful conditions [16,34]. Furthermore, varying sensitivity in fish behaviour, for example, under ocean acidification conditions, might be due to changes in the brain transcriptome [16]. Likewise, at natural CO_2 vents, changes in brain transcriptomes were observed across different species of Pomacentridae along with an accelerated evolution of genes involved in differentially expressed pathways, such as the circadian clock, acid-base regulation, and ion transport [35,36]. More work is needed to understand whether a species' adaptation potential will also benefit population and ecosystem levels and whether selection of specific traits under changing environmental conditions will alter the ecology and population structure of fish assemblages.

Organismal ecology

Studies on the impact of climate change stressors at the organismal levels typically assess how individual traits altered. These include changes to their growth, mortality, reproduction, morphology, movement, and various behaviours. They also cover the degree of plasticity of such traits in response to changing environmental conditions either within or across generations.

Phenotypic plasticity

There is now strong evidence that fishes can show some degree of physiological, morphological, or behavioural plasticity in response to ocean acidification and warming, and most predominantly within a generation (reviewed in [37,38]). Such developmental plasticity is perhaps unsurprising in fish considering the prevalence of their bipartite life cycles, since this form of plasticity is theoretically favoured when offspring are likely to experience conditions distinct from their parents [24]. There is also growing evidence that in cases where full compensation is not possible within a generation, parental effects and transgenerational plasticity can restore or improve phenotypes (beneficial plasticity) beyond what is possible within a generation [39]. For example, in the spiny chromis damselfish only partial compensation of aerobic metabolism was possible with developmental thermal plasticity [25] and full restoration back to control levels was possible with transgenerational warming [40]. However, beneficial plasticity to environmental change does not always occur, with limited plasticity of behaviour and reproductive capacity in response to both ocean warming and acidification within a few generations [37,39]. Even with parental exposure to elevated CO_2, negative impacts to

antipredator behaviours remained [41], suggesting that adaptation via inheritance of CO_2 tolerance may be critical [16] (Schunter et al. 2016).

(Eco)physiology

Ecophysiological responses to stress resulting from climate-driven changes to an organism's environment can be expressed at primary, secondary, and tertiary levels within individuals, which include the physiological mechanisms and behavioural changes that an organism uses to re-establish and maintain homeostasis under stress [42]. At the primary physiological level, stress responses are largely neuro-endocrine and involve the release of catecholamines and corticosteroids (glucocorticoids) [43].

At the secondary physiological level, heat shock proteins (HSPs) and haematological responses are initiated that activate metabolic, cardio-respiratory, immune, and ion-balance changes [44]. For example, tissue biomarker responses to a simulated heatwave, such as changes in red muscle citrate synthase and lactate dehydrogenase activities, blood glucose and haemoglobin concentrations, spleen somatic index, and gill lamellar perimeter and width, occurred within the first week of exposure in the more active, mobile fish species (*Caesio cuning*), but were reduced and delayed in the more sessile, territorial species *Cheilodipterus quinquelineatus* [45].

Tertiary physiological responses are often at the whole-organism level and can affect growth, movement, reproduction, and resistance to disease [46]. Stress responses can be immediately beneficial (e.g., fight or flight), adaptive over the longer term [47], or maladaptive to alter growth, feeding, digestion, immune function, and/or reproduction [48]. For example, Nagelkerken et al. [13] (2021) observed higher survival, reproduction, and feeding, but no noticeable changes in growth rates, energy storage, antioxidants, oxidative damage, or protein content in some species of temperate triplefins (Tripterygiidae) at natural CO_2 vents compared to areas with present-day levels of pCO_2. Hypoxia shows stronger negative responses, on average, compared to warming and acidification, on the metabolism, growth and survival in fishes, whilst warming mostly increases metabolic rates [49].

Physiological responses to climate change will vary by species, life histories, life cycle, activity, or tolerance levels [12], and bioregions [27], but also temporally. Changes in gene expression patterns can be modulated by metabolism, immune function, and HSP production [32]. Hence, while primary, secondary, and tertiary stress responses to individual climate change stressors are becoming clearer, little is still known about how the vast diversity of fish species will physiologically respond to concurrent climate change stressors and their scope for physiological acclimatisation and adaptation [50].

Behavioural ecology

Besides changes to physiology, behavioural modification is also considered one of the first key responses by fishes to environmental change [51]. Ocean acidification, warming and hypoxia can all interfere with the way fishes process sensory information through olfaction, audition, and vision [52–54]. For elevated CO_2, this has been attributed to malfunctioning neurosensory systems in damselfishes [55] and coho salmon (*Oncorhynchus kisutch*) [56], leading to impairment of a suite of fitness-enhancing behaviours (e.g., shoaling, foraging, predator evasion, habitat selection, and defence), which in turn depends on species-specific sensitivities to stressors [17,57]. Shoaling is a particularly important aspect of fish behavioural ecology given most fish species shoal during at least part of their life cycle [58]. However, exposure to climate change stressors can negatively affect behavioural and sensory traits that underpin shoaling behaviours [59,60]. This can lead to reduced shoal mate familiarity [61], reduced lateralisation

[62], and slower swimming speeds [63], resulting in disrupted group formation [64], all of which can lead to decreased fitness [58].

To date, most studies investigating the effects of climate change on fish behaviour have been reductionist in nature, using a single stressor under static conditions. Recent advances have allowed for experimental conditions to better mimic those of natural environments [65], including the use of complex mesocosms [66] or natural analogues of climate change [67,68]. Most behavioural studies have also focussed on single species, limiting our understanding of how behavioural changes of multiple interacting species can affect communities and food webs [69]. Upscaling species- to community-level behavioural responses to multiple stressors is required for a more comprehensive and realistic picture of the effects of climate change on aquatic communities [2].

Movement ecology

Behavioural responses to climate stress can also induce fish movement and migrations. Site-attached or small-range species that cannot escape their direct environment will need to rely on physiological acclimatization to climate-change stress. However, species with greater mobility may be able to avoid stressful environmental conditions by relocating [70]. For example, lake trout (*Salvelinus namaycush*) can seek out cooler groundwater refugia during late summer when the lake more generally exceeds preferred temperatures [71]. Consequently, physiological sensitivity, as determined from aquarium-based manipulations, might overestimate the impact of climate change as observed in nature [72]. Likewise, some species can avoid rapid environmental change by extending their ranges to higher latitudes, deeper waters, or occupy climate refugia (see *Landscape ecology*). However, diadromous species that move between the ocean and freshwater might experience reduced movement due to hypoxic zones in estuaries functioning as a chemical barrier [7]. In comparison to terrestrial ectotherms, we know very little about how small-scale movement may allow aquatic species to buffer the negative impacts of environmental change through processes such as behavioural thermoregulation.

It is also crucial to consider climate impacts on spawning migration and behaviours, as reproduction has evolved to generally occur within a species-specific, narrow environmental window and via environmental cues that determine breeding timing and synchronisation. Environmental change can reduce the length of the spawning season [73], alter the quality and quantity of progeny, and instigate ecological trade-offs [13,74]. Many species use thermal cues, often combined with other environmental cues (e.g., lunar, rainfall), to determine timing of migration and spawning [75]. Phenological shifts could allow reproduction to still occur with suitable physiological windows; however, this may result in a mismatch with the timing of lower trophic levels that are essential for early life stages [76]. For example, effects of ocean warming from the late 1970s has led to decreased population recruitment of glass eels (*Anguilla* spp.) due to reduced primary production and food for larvae [77]. Much of the knowledge on reproductive movement is focused on fisheries species, which are well monitored for stock assessment and management; yet, potential impacts to non-fisheries species remain largely unknown.

Population ecology

Climate stress impacts on individuals will have flow-on effects on their populations. The degree and type of phenotypic plasticity and genotypic diversity across individuals belonging to a population will play a key role in the natural selection of more climate-resilient

individuals. If their climate-resilient traits are hereditary, they can be passed on the next generation and create more climate-resilient populations of a particular species.

Population growth and demography

Due to the rapid rate of climate change, the demography and life histories of fishes can play a substantial role in their ability to persist under environmental change. Attributes including long generation time, delayed maturity, low fecundity, and poor offspring provisioning could all reduce the adaptive capacity of fish to climate change and alter population abundances and size structures [78,79]. As predicted by the temperature-body size theory, ocean warming is likely to reduce maximum body sizes and increase somatic growth rates in general, but not always [80], with significant consequences for the demography of fish populations [81]. Likewise, altered recruitment rates due to increased larval mortality under climate change stress or phenological mismatches with required prey will modify fish population dynamics [82]. Furthermore, as waters warm, food requirements increase with fish metabolism, thus exacerbating resource limitations on population growth of some species [10]. For example, Koenigstein et al. [83] used an integrative model that included physiological life history responses, and forecast recruitment failure for Atlantic cod (*Gadus morhua*) under ocean acidification and warming, although some of the negative effects might be mitigated via increased food abundance. Severe hypoxia is often associated with mass fish kills, whilst reduced dissolved oxygen concentrations can also alter prey abundances leading to modified predator-prey interactions [84].

Community ecology

Responses at the population level will affect the demography of fishes and the size of their populations, but does not include the effects of other species (e.g. predators, competitors, parasites) on their abundances. At the community level, these species interactions are key drivers on species abundances, diversity and community compositions.

Competition and species interactions

As the environment changes, so do the complex processes and species interactions that shape communities [2,85]. Based on the premise that natural selection drives organisms toward optimising reproductive success, mathematical game theory has increasingly been applied to analyse the evolution of phenotypes as the environment changes [86]. At its simplest, game theory can be applied to pairwise competition between individuals based on differences in behaviour, size, age, and sex status, with game theory predicting whether a behavioural strategy is evolutionarily stable [87]. However, exposure to climate stressors (warming, acidification as well as hypoxia) can disrupt these processes owing to changes in food availability [88], predator-prey interactions [89,90], competition for habitat [91,92], and habitat selection [93], leading to food web and community destabilization [94,95].

Environmental warming due to climate change can alter intra- and interspecific competition [96], whilst in damselfishes elevated CO_2 can reverse competitive dominance, particularly in degraded coral habitat [91]. Likewise, for estuarine fishes with different growth-temperature relationships, even slight warming can switch the ranking in growth rates [97]. Kingsbury et al. [98] showed that range-extending coral reef fishes modified their niches in the presence of temperate species, presumably avoiding competition. Similarly, density-dependence of key fitness characteristics of fishes may alter as oceans warm. For example, Watson et al. [99] showed that the positive effect of temperature on growth rates was lower at high fish population densities compared to lower fish density of freshwater *Galaxias maculatus* populations.

Climate change can simultaneously exert both negative and positive changes to community structures, suggesting that indirect effects of climate change may alter the interactions between strongly linked species [8,10] (Ockendon et al. 2014, Nagelkerken and Connell 2015).

Niche specialisation

Niche specialisation constrains the capacity of species to persist in places with altered environmental conditions. For example, habitat and diet specialisation are expected to put species at risk when resource requirements are not available in the altered environment [100]. This results in the expectation that generalist species will often fare better with climate change [101]. Much of the research on fish supports this; for example, the narrow ecological niche of range-restricted and endemic freshwater species put them at greater risk of future extinction [102]. Freshwater fishes also have reduced potential to disperse to more favourable habitats when compared to marine fishes, which is often exacerbated by human development (e.g., weirs, dams). Tropical coral reef fishes are well studied in relation to their specialization on coral habitat, with clear impacts of coral loss both for highly specialised and more generalist fish species [103]. Some of the observed impacts to more generalist species are likely due to indirect effects, for example, through relief from predators and boosted prey resources that benefit generalist benthic fish species more than specialists on temperate rocky reefs [67].

Symbiosis, parasitism, and disease

The myriad types of symbiotic relationships among fishes and range of taxa represented preclude generalisations to be made as to the impacts of ongoing climate change. Yet, what is likely is that the effects to hosts and symbionts will be altered but not uniformly [104,105]. Of these relationships, parasitism–due to the often-cryptic nature of parasites–has remained understudied amongst fishes, especially when it comes to interactions with climate change stressors. Nevertheless, habitat loss, reductions in water quality, and top-level predator removal that are co-occurring with climate change are predicted to increase the risk of parasitism, exacerbate interactions between fish and parasites, and ultimately impact fish survival [105,106]. Some of these effects may be due to both dopaminergic and seratoninergic neurological impairment that for example can decrease the interactions between tropical cleaner wrasses (*Labroides dimidiatus*) and their client fishes (*Naso elegans*) in response to ocean warming and acidification conditions, thereby increasing the risk of parasites due to degradation of the cleaner-client mutualism [107]. Moreover, under acidification conditions, fish incur a significant metabolic cost when they do not have access to cleaning stations [108], which could increase vulnerability to parasites and disease. These responses become even more complex when the survival of some parasites (e.g., gnathids) is unaffected by ocean acidification conditions [109], thereby emphasizing the non-uniformity in responses within these relationships. Hypoxia can negatively affect the immune response and physiological functioning of fishes making them more susceptible to disease [110].

Similar trends also exist in mutualistic relationships and could lead to increased disease prevalence. For example, under ocean acidification juvenile fishes may spend less time in their protective symbiotic relationships with jellyfish [111], and anemonefishes incur significant metabolic costs (~8%) when their symbiotic anemones are bleached due to ocean warming and marine heatwaves, which could explain decreases in their spawning and fecundity [112]. These altered symbiotic relationships as well as the role that climate change stressors, habitat degradation, and poor water quality directly play on fish health explain, in part, the dramatic rise in diseases in the marine environment due to global climate change [113].

Landscape ecology

Fish responses at landscape level include alterations to the landscape, including widely observed changes to habitat structural complexity and habitat composition under warming and acidification. In addition, spatial processes that operate at landscape levels can have strong influences on fishes and their communities, e.g. through altered larval dispersal and species range extensions or range contractions under warming.

Larval dispersal

Most marine fishes disperse through larval transport via ocean currents, and hence strengthened poleward boundary currents due to climate change could increase physical dispersal of larvae on these currents and enhance range extensions and gene flow [114]. On the other hand, increasing sea temperatures often shorten pelagic larval duration (and can also increase survivorship) which could lead to decreased larval dispersal kernels, and reduced population connectivity due to a higher degree of self-recruitment [115]. Irrespectively, warming oceans are increasing tropical larval settlement and survival in temperate ecosystems, with successful species characterised by life history traits such as smaller maximum length and reduced age and length at maturity [116].

Tropicalisation and borealisation of cold water communities

As many species shift their distribution poleward in response to climate change, the proportion of 'warm affinity' species within fish communities has markedly increased in many regions of the world, a process known as 'tropicalisation' [117]. This tropicalisation can strongly impact the trophic structure of fish assemblages. In warm temperate reefs, tropicalisation has led to striking increases in the proportion of herbivorous as well as omnivorous fish biomass [118,119]. Interestingly, these changes in trophic structure observed on tropicalising reefs mirror patterns observed along latitudinal gradients, where warmer tropical latitudes are typically also characterised by a greater proportion of herbivores [120,121]. Species that are most successful in extending their range are often also either habitat [101], behavioural [122], or dietary [123] generalists.

In the Arctic, warming has led to the expansion of boreal fish communities toward the poles, a process coined 'borealisation' [124]. In the northern Barents Sea, large migratory fish predators and small planktivores are increasing in abundance, and small benthivores are declining, which is increasing their relative importance in the pelagic food web [124,125].

Range-extending fishes as ecosystem engineers

Climate change impacts the role of fish as ecosystem engineers by altering the intensity or direction of trophic interactions. For example, greater herbivory–driven by the range expansion of warm-affinity fishes such as species of parrotfishes (Scaridae), surgeonfishes (Acanthuridae), rabbitfishes (Siganidae) and drummers (Kyphosidae)–has led to the overgrazing of canopy-forming seaweeds or seagrasses [126]. Marine macrophytes are the foundation vegetated habitat of temperate systems. As such, their decline can have major cascading impacts on benthic communities and fish assemblages. For instance, in the eastern Mediterranean the loss of habitat-forming seaweeds caused by the range expansion of two *Siganus* species has been linked to a decrease in both fish species richness and abundance [127]. In Australia, increases in fish herbivory have also been linked to the decline of dominant kelp forests and the maintenance of turf-dominated reefs [128,129]. Coni et al. [68] observed that overgrazing of kelp by sea urchins (*Centrostephanus rodgersii*) created barrens that are

favoured by range extending fishes (in particular *Acanthurus* spp. and *Abudefduf* spp.) compared to native kelp habitat. However, many of these changes may represent a transitional state, and recent evidence shows the apparent tropicalisation of fish and benthic communities in regions like Japan can somewhat be reversed by elevated CO_2 [130] and by extreme cold events which are also predicted to increase under climate change [131].

Ecosystem ecology

At the level of ecosystems, altered food web structures, productivity, consumption rates, and energy flows across trophic levels have been observed. These can alter individual growth, reproduction and survival rates, as well as create altered species interactions (e.g. competition for food or altered predator-prey dynamics) with ensueing effects on species community composition, diversity and ecosystem productivity.

Trophodynamics and energy flow

Increasing herbivory in tropicalised reefs can increase the flow of energy to higher trophic levels, potentially leading to increases in benthic fish productivity [119,132]. In the Mediterranean Sea, however, increases in the proportion of herbivorous fish have been linked to a reduction in total fish biomass [127]. Tropicalisation and increased herbivory are also associated with enhanced production of detritus via increased defecation [133], thus impacting nutrient cycling and benthic microbial communities [134]. The physiological mechanisms underpinning these patterns are unclear, as there is little evidence that low temperatures disadvantage the digestion of algal or plant materials [135]. In the Arctic, food web properties are increasingly resembling those of boreal food webs, with a greater relative importance of pelagic species [125]. Novel feeding interactions between range-expanding and resident Arctic species are predicted to amplify the impact of species redistributions [136]. Ocean acidification can modify food web structures and energy flow, with elevated CO_2 generally acting as a nutrient for algae, boosting food webs through bottom-up effects [137]. However, ocean acidification and warming combined can constrict food webs at mid-levels, eventually leading to the collapse of top levels, fewer trophic levels, and a bottom-heavy food web [94]. Hypoxia can alter the community and size structures of zooplankton, resulting in altered food wen interactions with potential impacts on foraging, consumption and growth in fishes [138].

Macro-ecology

Large-scale patterns in biodiversity

Biogeographic patterns that have persisted for millions of years are likely to change through the next century in response to global change and overexploitation [139,140]. Climate impacts are even affecting the most notable biogeographic property known for fishes–the 'latitudinal gradient in biodiversity', with greater fish species richness in the tropics at both regional (gamma diversity) and site (alpha diversity) scales [141]. Nevertheless, marine richness dips at the equator, with maximal species richness evident at ~15˚ latitude North and South [142]. Through the past half century, richness has apparently declined on the equator and risen in mid-latitudes [70], with outcomes attributable to species emigrating poleward due to climate change [143].

The trophic composition of fish communities is changing in parallel with broad-scale changes in species richness. The proportion of species with particular traits shows predictable variation with species richness, including a higher proportion of planktivorous, small-bodied and pelagic fishes in locations with high species richness [144,145]. Identifying and

understanding variation in trait composition represents a challenging but important field of fish ecology, given the prominent influence of traits on metapopulation and food web dynamics. However, field observations are needed across large spatial scales, which might be achieved through citizen science [146] and by capitalising on rapid advances in metagenomic sample collection and processing [147].

Functional diversity and ecosystem stability

Fish functional diversity tends to decrease with climate change, leading to functional convergence toward traits that are more adapted to novel environments [148]. Such patterns have emerged in marine [148], estuarine [149], and freshwater [150] fish communities, with long-lived species with late maturation and/or large body sizes being disproportionately impacted [139,151]. However, different proxies of functional richness can sometimes show opposing effects to climate change stressors, highlighting the importance of testing complimentary measures of diversity [152]. Higher functional redundancy (i.e., higher number of species with similar ecological functions) can initially buffer communities against the detrimental impacts of climate disturbance [153], yet the general trend over time is a decrease of functional redundancy with, for example, a disproportionate loss of piscivores and fish species with pelagic eggs in the North Sea [148]. Reduced functional diversity can, in turn, impact ecosystem stability and increase the risk of losing important ecosystem functions through biotic homogenization and the loss of ecological specialists such as some species of gobies (Gobiidae) [101].

Furthermore, reduced oxygen carrying capacity at higher temperatures coupled with increased nutrient runoff from catchments can lead to establishment of anoxic 'dead zones'. These are now a global phenomenon, with an exponentially increasing footprint, and affecting a total ocean area estimated to be $> 245{,}000\ km^2$ in 2008 [154].

Fisheries ecology

Alterations to individual fitness and population sizes of targeted fisheries species can have flow-on effects on seafood production. Moreover, with species shifting their biogeographic ranges under ocean warming, populations of fishes species are relocating to other areas, which can have socio-economic effects on local fishermen as well as commercial fisheries.

Fisheries production

Mounting evidence suggests complex impacts of climate change on fisheries production, resulting from the adverse effects of single climate stressors (e.g., global warming, ocean acidification, extreme weather events), as well as their cumulative impacts and interactions with other human pressures (e.g., overexploitation, pollution) [155]. Globally, changes in ocean conditions have been linked to a reduction of body size in commercially important marine fishes (e.g., Atlantic cod *Gadus morhua*), potentially impacting global fisheries catches [156]. Weather extremes, such as floods and droughts, are also increasingly impacting estuarine ecosystems on which many freshwater and marine species rely for at least part of their life cycle [7,149]. Furthermore, climate-driven species range shifts progressively redistribute fish stocks, leading to both species extinctions and invasions that are projected to increase in the future [157]. Therefore, many species will likely shift across national and other political boundaries in coming decades, creating potential for conflict over newly shared resources, as previously observed with Pacific salmon (*Oncorhynchus* spp.) stocks [158]. Although potential adaptive strategies arise for fisheries under climate change, future research is urgently needed to identify barriers, constraints, and limits for climate adaptation [155]. Furthermore, most research has so far considered climate change as a single macro-stressor [155], and the direct effects of

other stressors (e.g., ocean acidification, hypoxia) have mostly remained inconclusive and require further research [159].

Fish nutritional quality

Fish are a rich source of essential nutrients, such as iron, zinc, Omega-3 fatty acids, and vitamins, that support human health and provide an important pathway for tackling micronutrient deficiencies in many countries [160,161]. Yet, ocean warming and acidification have the potential to alter fish nutrient concentration through both direct (metabolism, nutrient assimilation efficiency) and indirect (nutritional quality and composition of basal food sources) effects [162]. However, divergent nutritional responses to climate change among species and functional groups suggest the emergence of 'winners' and 'losers' of climate change among species targeted by fisheries [163]. For example, herbivorous rabbitfishes (Siganidae) caught on regime-shifted macroalgal habitats after mass coral bleaching were enriched in iron and zinc [163]. This contrasted with experimental research on a euryhaline fish, the yellowfin bream (*Acanthopagrus australis)*, that showed no effects of future ocean conditions on fish nutritional content, possibly linked to its broad habitat distribution and greater physiological tolerance [164]. Therefore, an important mechanism for future fisheries adaptation will be to identify the species that are most likely to sustain food and nutrition into the future and reorientate fisheries management accordingly [165].

Conservation ecology

Conservation of most species is best achieved through spatial mechanisms that protect many species within whole ecosystems–that is through 'marine protected areas' (MPAs) where adverse pressures are reduced as much as practical [166]. All of the many potential benefits of MPAs, including biodiversity conservation, insurance against fisheries collapse, recreation, aesthetic enjoyment, and educational opportunities [167], are potentially compromised by climate change, including interactions with other stressors [168]. Ocean warming leads to loss of fish populations from MPAs as species track preferred sea temperatures toward the poles, while extreme heatwaves can cause loss of essential fish habitats including coral, kelp, mangrove, and seagrass habitat structure. Furthermore, ocean acidification potentially affects organisms with calcareous structures, and rising sea level affects intertidal fish species, particularly when the shore is bounded by urban development that prevents landward progression [169].

A global analysis by [170] identified a widespread mismatch between climate vulnerability of recreational fishes and conservation effort, with most effort focussed on marine fishes of high socio-economic value and little effort on freshwater and diadromous species. A first step toward minimising species loss is the amelioration of local compounding stressors [171]. Another partial solution involves consolidating MPAs into networks, where individual parks operate as stepping stones that assist species in translocating poleward [172]. Restoring degraded coral reefs, kelp forests, seagrass beds, shellfish reefs, and mangroves will also be necessary for the long-term recovery of habitat-dependent species [173]. However, excessive cost has restricted restoration efforts to local scales [174]. Identifying and protecting potentially resilient areas, and integrating climate change into MPA planning and evaluation, are also fundamental if healthy ecosystems are to be maintained [175].

Scaling up from genes to ecosystems

Scaling up from organismal-level impacts of climate change on fishes to those at the population- and community-levels is challenging and requires incorporating the mediating effects of species traits and natural ecological processes across biological levels from genes to ecosystems (Fig 3). All levels of biological organisation are interconnected, either directly, or via other

pathways. For example, genomic responses may allow species to adjust their physiology to cope with climate stress, and as such maintain their physiological performance and homeostasis, which would reduce climate-driven alterations to their fitness and consequently community structuring and food web dynamics. Yet, because of the many interconnected direct and indirect pathways, it is more likely than not that some degree of change ensues from one or more climate stressors. Such changes may facilitate novel ecological interactions, novel community structures, and rewired food webs. In-depth studies at several natural analogues have already shown modifications to occur at more than one level of biological organisation under the effects of ocean warming (e.g., [68]–community and landscape ecology), ocean acidification (e.g., [13,67]–behaviour, physiology, demography, competition, niche specialisation, trophodynamics, biodiversity, and habitat change), or hypoxia (e.g., [176]). However, these studies have also identified the inherent complexity in accurately predicting fish responses to climate change.

Because species all have their unique ecological niches, environmental tolerances, behavioural repertoires, and adaptive capacities, different species or populations will respond to climate change in very different ways. Yet, effective management and conservation to address the effects of climate change requires insights that can be generalised and consistent across multiple taxa and biogeographies (e.g. Table 1). Such broader insights into somewhat predictable or consistent responses are necessary to inform climate adaptation strategies before further effects of climate change emerge, and may be acquired through some of the approaches as discussed below.

Natural analogues that incorporate ecological complexity

Integrating responses at multiple levels of biological organisation is inherently difficult to study in laboratory settings, but natural laboratories that mimic future climate conditions (e.g., volcanic CO_2 vents, ocean warming hotspots, natural environmental gradients such as upwelling areas) can incorporate (part of) such ecological complexity. This is important because ecological complexity can buffer negative impacts of climate stressors such as those observed in more simplified laboratory systems [66]. Moreover, natural variability (e.g., daily, seasonally) of climate stressors–which is mimicked at natural analogues–is known to alter species responses to climate stress (e.g., diminished fish gene expression in *Embiotoca jacksoni* compared to stable stressor conditions [177]). Especially for species with restricted home ranges, these analogues allow insights into the integrated ecological responses of fishes to climate change stressors, responses like epigenetic adaptation, behavioural modifications, physiological acclimatization, phenological responses, demographic changes, range shifts, species interactions, habitat regime shifts, and natural selection, all of which combine to explain how communities, ecosystems, and biodiversity might be reshaped directly and indirectly by environmental change [178]. They also have their drawbacks, such as single stressor effects, small spatial scales, and species influx from adjacent systems that reflect present-day conditions. However, studies have attempted to address some of these issues for fishes, for example, by working on site-attached species [67], performing meta-analyses of natural analogues [18], or by combining analogues that reflect different climate stressors (e.g. [68]).

Generalisable trends from meta-analyses

Meta-analyses represent a powerful tool to predict species responses to climate stress and their consistency across functional groups, biogeographies, and ecosystems. However, they are still heavily restricted to specific subfields of fish ecology, such as ecophysiology, and at the level of individual organisms (S1 Table, Fig 1). Some authors have used quantitative meta-analyses to

Table 1. The effects of climate change stressors on the ecology of fishes—Key responses.

Subfield	Ocean warming	Ocean acification	Hypoxia
Molecular plasticity and (epi)genetic adaptation	Some fish species rapidly adapt to ocean warming by adjusting their metabolic pathways at molecular level and transfer this information to the next generation via selective DNA methylation of specific loci	Fish respond to ocean acidification by altering the expression of circadian clock genes in the brain. This process is controlled via the differential expression of epigenetics pathways	Various studies observed altered gene expression in fishes exposed to hypoxia. Hypoxia can have negative effects on reproduction through transgenerational and epigenetic effects
Phenotypic plasticity	Numerous species show capcity for developmental and transgenerational plasticity to compensate negative effects on a range of traits	Plasticity of physiological and morphological traits is possible, however, plasticity of behaviour to ocean acidification might be more limited	Developmental plasticity in relation to hypoxia is found in morphological and physiological traits that affect cardiovascular capacity and oxygen uptake
(Eco)physiology	Acute warming (e.g., heatwaves) can increase metabolic costs and enzyme activities, and change haematological properties and gill morphology to maintain oxygen uptake and adequate delivery to the tissues. Gradual warming will result in similar adjustments over the longer term and/or changes in the timing of key life history milestones, such as reproduction, and distribution patterns	The eco-physiological responses of fish to ocean acidification conditions stem from the ion imbalance and acid-base regulatory mechanisms aimed to maintain oxygen transport whilst restoring homeostasis. Such imbalances in the brain, however, can result in altered function of GABA-A neurotransmitter receptors that can alter an array of behaviours	Hypoxia can have severe effects on the immune response and physiological function of fishes, including feeding, energy production, growth, metabolism, reproduction, and development
Behavioural ecology	Warming can affect the neural processing that underpins the processing of important environmental cues. This can lead to changes in behaviour and the way in which species interact	Ocean acidification mostly impacts sensory performance due to malfunctioning neurosensory systems. This can lead to a suite of behavioural impairments, affecting the way in which species response to cues. However, this is dependent on species-specific sensitivities to stressors	Hypoxia interferes with the way fishes process sensory information. This can lead to changes in behaviour and the way in which species interact, including schooling
Movement ecology	Fish can use movement to avoid poor thermal conditions and even thermoregulate. However, the amount by which they can do this depends on other ecological traits, such as territoriality and site attachment	Fish experiencing ocean acidification in the short term tend to be more bold and can increase activity levels affecting movement on small spatial scale	Fishes are known to use movement to avoid hypoxic conditions. If movement is not possible, low dissoved oxygen can result in altered movement and swimming, or large scale mortality events
Population growth and demography	Ocean warming is predicted to reduce maximum body sizes and increase somatic growth rates, with significant consequences for the demography of fishes. Warming will also lead to changes in development rates that may result in phenological mismatches with prey availability	Ocean acidification may impact the avaliabilty and species identity of lower-trophic food such as phytoplankton, zooplankton, and benthic algae, exerting bottom up control on fish populations	Hypoxia can lead to mass fish kills, leading to local reduction of populations of more sensitive species
Competition and species interactions	Increased metabolic demands can alter trophic interaction strengths. Food web alterations can also be altered through novel community compositions resulting from species range shifts	Relatively few strong direct effects, mainly indirect effects through altered habitat composition, altered food abundance, and modified species communities	Changes in community structures due to loss of sensitive species and increases of hypoxia-tolerant species
Niche specialisation	Niche shifts (habitat, diet, behaviour) leading to reduced or increased overlap with other species	Niche shifts (habitat, diet, behaviour) leading to reduced or increased overlap with other species. Generalist species can benefit via population growth	Physiological generalist (tolerant to hypoxia) prevail
Symbiosis, parasitism, and disease	Risks of parasitism and disease will increase with warming, as will metabolic costs. There may also be neurological impairments that alter such relationships. Warming will also result in habitat degradation and poor water quality, which will also increase disease prevalence.	Altered relationships due to ocean acidification conditions could increase disease prevalence, lower immunity, and increase metabolic costs. Some symbiotic relationships are weakened due to ocean acidification	Low oxygen conditions in some areas can lead to an increase in disease prevalence and a breakdown of symbiotic relationships. Acute hypoxia can instigate the adrenergic stress response, which over the longer term, could lead to chronically elevated corticosteroid, lower immunity, and increased disease prevalence and susceptibility to parasitism
Larval dispersal	Some species will show shorter dispersal periods but faster swimming (also aided by poleward currents)	Larvae of some species might show decreased feeding, pelagic larval duration, growth, or survival rates	Potentially decreased pelagic larval duration and decreased larval survival

(*Continued*)

Table 1. (Continued)

Subfield	Ocean warming	Ocean acification	Hypoxia
Tropicalisation and borealisation of cold water communities	Enhanced winter survival and range expansion into higher latitudes	Ocean acidification may oppose (directly or indirectly via negative impacts on range-extending corals or through reduction of kelp-overgrazing urchins) range expansion of tropical species into temperate areas due to warming	Hypoxia may be more tolerated by alien species and poleward invading tropical fishes than their local temperate competitors or predators
Range-extending fishes as ecosystem engineers	Altered trophic interactions linked to species redistributions of fish can cause ecological regime shifts, e.g. increased herbivory in temperate reefs due to range expansion of tropical herbivores can cause declines in habitat-forming kelp	Ocean acidification may reduce kelp cover in favour of turf algae, altering the impacts of range-extending herbiores on benthic vegetation	Hypoxia in combination with warming may accelerate poleward shifts in distribution and enhance their ecological impacts
Trophodynamics and energy flow	Shifts in trophic interactions due to warming can alter flows of energy and the relative importance of benthic and pelagic food webs	Changes in food web structure and energy flow due to impacts on habitat-forming primary producers (bottom-up effects) and potential collapse of top trophic levels	Hypoxia can increase the trophic niche of fish species and alter trophic interactions in multiple ways, impacting both predation rates on fish larvae as well as consumption rates by fish
Large-scale patterns in biodiversity	Mixing of temperate resident specie and tropical species moving to higher latitudes (increased diversity initially); loss of species that are prevented by oceanographic or physical barriers from moving poleward; unpredictable interactions between species within 'novel communities' as species move at different rates	Reduced survival of many species; trophic compositional changes as the productivity and composition of primary producers changes with loss of calcifiers; flow-on conesquences of changing habitats affecting associated species	Expansion of 'dead zones' across large geographic scales
Functional diversity and ecosystem stability	Loss of functional diversity and functional redundancy under climate change	Loss of functional diversity and increased biotic homogenisation. Ecosystem simplifaction, often towards domination of generalist or weedy species	Fish community simplification and diversity loss can reduce ecosystem stability
Fisheries production	Fish stock redistribution, reduction in fish abundance and biomass	Direct effects on finsfish fisheries production are generally inconclusive, but indirect effects are likely	Hypoxia contributes to reduction in fish body size and stock redistribution
Fish nutritional quality	Warming to affect fish nutrient concentration through direct and indirect effects; impact is highly variable among species	Indirect effects through changes in phytoplankton community composition; little effect on euryhaline fish	Indirect effects through changes in metabolism
Marine protected areas and conservation priorities	Need to consider migration of species into and out of MPAs; increase efforts to reduce cumulative stressors (e.g. fishing, pollution) that add to climate change impacts	Need to prioritise conservation of species most affected; consider potential habitat shifts when identifying and managing MPAs	Need to locate MPAs outside expanding dead zones, with priority for areas with good water movement

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test the degree to which species responses are in accordance with previous (modelled) climate change forecasts (e.g., [1,14,179]). Meta-analyses can suffer from publication bias (i.e., toward reporting only detectable effects), but with the uprise of open access journals that publish studies based on methodological and analytical rigour rather than novelty or significant effects, this effect is likely to diminish. However, meta-analyses are insufficient to forecast fish responses to climate change across multiple levels of biological organisation and across time. Advanced ecological modelling approaches could be used for this purpose.

Holistic ecological models for more accurate future predictions

The various ecological models forecasting fish responses to climate change–species distribution models (SDMs), food web models, whole-ecosystem models, bioenergetic models, and dynamic bioclimate envelope models, to name a few–vary along a gradient of model

complexity, each with specific objectives, strengths, and weaknesses. At the simplest end of the spectrum, SDMs only require species occurrences matched with associated environmental conditions to determine a species' habitat suitability over time and space. The relative simplicity of SDMs has led to many applications for fish communities across ecosystems and bioregions [180]. However, the ability of SDMs to forecast species distributions under future conditions remains controversial [181] because they assume stable species-environment relationships, which can be violated by adaptive mechanisms such as plasticity (but see [182]). In their original implementation, SDMs also do not account for species interactions, which can instead be achieved by food web models [183,184]. Food web models quantify the flow of energy and biomass through ecosystems, yet their parametrisation for complex ecosystems remains difficult and is rarely spatially explicit (but see [185,186]). Integration of SDMs and food web models thus represents a promising avenue and has previously been used to forecast changes to fish species richness and their trophic linkages (e.g., in the Mediterranean under warming [187]). Whole-ecosystem models such as Atlantis can incorporate biophysics, socioeconomics, management, and human impacts to forecast changes in fish biomass of functional groups (e.g., [188]). Bioenergetic models (e.g., Dynamic Energy Budgets) are suitable to predict how different physiological processes interact at the organismal level [189]. However, due to the large amount of data used to parametrize these models, most applications remain restricted to a few well-studied and commercially exploited species. To date, dynamic bioclimate envelope models likely represent the most integrative models, e.g., combining spatially explicit population dynamics with a bioclimate envelope model for >1,000 exploited invertebrate and fish species at a global scale [157].

Next-generation models need to be developed that integrate adaptive responses of fish to climate change across multiple levels of biological organisations as well as changing species interactions and behaviours (e.g., [190]). Although no model can integrate fish responses to climate change across all biological levels simultaneously, a better identification and parametrisation of important responses at relevant spatiotemporal scales, particularly through meta-analyses, will be necessary to construct future ecological models in support of fisheries management and biodiversity conservation. Improved compatibility between models and collaboration between research teams should also allow to combine models predicting responses at various biological levels and, importantly, validate model predictions and quantify the uncertainty stemming from every model component.

Using past extreme climate events to predict the future

Past climate perturbations such as the Paleocene Eocene Thermal Maximum may provide clues about the impacts of climate change in the Anthropocene, although such events typically occurred across longer timescales than present climate change. Nevertheless, responses of modern-day marine taxa to ocean warming, acidification, and hypoxia align to those observed for fossils extinctions during the Phanerozoic eon [191]. Likewise, Avaria-Llautureo et al. [192] observed smaller-sized anchovies and herrings with lower dispersal ability during historical periods (during the past 150 Myrs) of warmers waters, as predicted by theory, whilst Salvatteci et al. [193] observed an ecological replacement of the present-day migratory anchovies with smaller-bodied fishes during the last interglacial period in a warmer, oxygen-poor ocean. A critical, yet often overlooked step in ecological modelling is model validation. Past extreme climatic events or periods of gradual climate change can be used retrospectively for this purpose, to inform about the potential responses of fishes to future climate.

Conclusions

Predicting what future fish populations and communities might look like will not be an easy task due to the various dimensions of change (time, space, traits, etc.) and the levels of biological organisation (and the interactions amongst these levels) affected for a highly diverse group of ocean fauna. Yet, the increasing meta-data on fish responses to climate change, advances in modelling and computing power, discovery of new natural analogues of climate change, and insights into the consequences of past extreme climatic events, will allow us to integrate these insights for more realistic predations of climate change effects on fishes. Elucidating generalisable species responses to climate change will be important to develop climate adaption management and conservation strategies. Fish communities of the future will be different from how we know them, but we need to make sure that under rapid environmental change we acquire the relevant knowledge for the management of species and their communities to sustain global biodiversity, fisheries productivity, and the critical ecosystem services that fishes perform.

Supporting information

S1 Table. Results of a literature search for meta-analyses on the effects of climate change on fishes in Web of Science on 19 October 2022. Search terms were: all fields 'meta analysis' and all fields 'climate change or warming or temperature or ocean acidification or carbon dioxide or elevated CO2 or reduced ph or hypox* or anox*' and all fields 'fish*'. Hypox* included hypoxia and hypoxic, whilst anox* included anoxia and anoxic. A few additional meta-analyses from our own paper collections were added that were missed in the literature search. Results needed to include an effect size, or a mean/median with error bars; papers with just regression graphs were excluded. OA = ocean acidification, OW = ocean warming, MR = marine, FW = freshwater. For the systematic reviews the same terms as for meta-analyses were used in Web of Science, except that 'meta analysis' was replaced with 'systematic review' as a search term. The semi-quantitative analysis of non-systematic review papers was based on a personal library (IN) accumulated during the past 11 years.
(XLSX)

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References

1. Scheffers BR, De Meester L, Bridge TCL, Hoffmann AA, Pandolfi JM, Corlett RT, et al. The broad footprint of climate change from genes to biomes to people. Science. 2016; 354: aaf7671. https://doi.org/10.1126/science.aaf7671 PMID: 27846577
2. Nagelkerken I, Munday PL. Animal behaviour shapes the ecological effects of ocean acidification and warming: moving from individual to community-level responses. Glob Chang Biol. 2016; 22(3): 974–989. https://doi.org/10.1111/gcb.13167 PMID: 26700211
3. Araújo MB, Luoto M. The importance of biotic interactions for modelling species distributions under climate change. Glob Ecol Biogeogr. 2007; 16(6): 743–753.
4. Brown CJ, Saunders MI, Possingham HP, Richardson AJ. Managing for interactions between local and global stressors of ecosystems. PLoS One. 2013; 8(6): e65765. https://doi.org/10.1371/journal.pone.0065765 PMID: 23776542
5. Froese R, Pauly D. FishBase; 2023. www.fishbase.org.
6. Holmlund CM, Hammer M. Ecosystem services generated by fish populations. Ecol Econ. 1999; 29 (2): 253–268.
7. Lauchlan SS, Nagelkerken I. Species range shifts along multistressor mosaics in estuarine environments under future climate. Fish Fish. 2020; 21: 32–46.
8. Ockendon N, Baker DJ, Carr JA, White EC, Almond RE, Amano T, et al. Mechanisms underpinning climatic impacts on natural populations: altered species interactions are more important than direct effects. Glob Chang Biol. 2014; 20(7): 2221–2229.
9. Duffy JE, Lefcheck JS, Stuart-Smith RD, Navarrete SA, Edgar GJ. Biodiversity enhances reef fish biomass and resistance to climate change. Proc Nat Acad Sci USA. 2016; 113(22): 6230–6235. https://doi.org/10.1073/pnas.1524465113 PMID: 27185921
10. Nagelkerken I, Connell SD. Global alteration of ocean ecosystem functioning due to increasing human CO_2 emissions. Proc Nat Acad Sci USA. 2015; 112(43): 13272–13277.
11. Pecl GT, Araujo MB, Bell JD, Blanchard J, Bonebrake TC, Chen IC, et al. Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. Science. 2017; 355(6332): eaai9214. https://doi.org/10.1126/science.aai9214 PMID: 28360268
12. Pörtner HO, Peck MA. Climate change effects on fishes and fisheries: towards a cause-and-effect understanding. J Fish Biol. 2010; 77: 1745–1779. https://doi.org/10.1111/j.1095-8649.2010.02783.x PMID: 21078088
13. Nagelkerken I, Alemany T, Anquetin JM, Ferreira CM, Ludwig KE, Sasaki M, et al. Ocean acidification boosts reproduction in fish via indirect effects. PLoS Biol. 2021; 19: e3001033. https://doi.org/10.1371/journal.pbio.3001033 PMID: 33465064
14. Poloczanska E, Brown C, Sydeman W, Kiessling W, Schoeman DS, Moore PJ, et al. Global imprint of climate change on marine life. Nat Clim Chang. 2013; 3: 919–925.
15. Veilleux HD, Ryu T, Donelson JM, Van Herwerden L, Seridi L, Ghosheh Y, et al. Molecular processes of transgenerational acclimation to a warming ocean. Nat Clim Chang. 2015; 5 (12): 1074–1078.
16. Schunter C, Welch MJ, Ryu T, Zhang H, Berumen ML, Nilsson GE, et al. Molecular signatures of transgenerational response to ocean acidification in a species of reef fish. Nat Clim Chang. 2016; 6(11): 1014–1018.
17. Kroeker KJ, Kordas RL, Crim R, Hendriks IE, Ramajo L, Singh GS, et al. Impacts of ocean acidification on marine organisms: quantifying sensitivities and interaction with warming. Glob Chang Biol. 2013; 19(6): 1884–1896. https://doi.org/10.1111/gcb.12179 PMID: 23505245
18. Nagelkerken I, Connell SD. Ocean acidification drives global reshuffling of ecological communities. Glob Chang Biol. 2022; 28: 7038–7048. https://doi.org/10.1111/gcb.16410 PMID: 36172974
19. Walden G, Noirot C, Nagelkerken I. A future 1.2 ˚C increase in ocean temperature alters the quality of mangrove habitats for marine plants and animals. Sci Total Environ. 2019; 690: 596–603.
20. Wittmann A, Pörtner HO. Sensitivities of extant animal taxa to ocean acidification. Nat Clim Chang. 2013; 3: 995–1001.
21. Cattano C, Claudet J, Domenici P, Milazzo M. Living in a high CO_2 world: a global meta-analysis shows multiple trait-mediated fish responses to ocean acidification. Ecol Monogr. 2018; 88: 320–335.
22. Messina S, Costantini D, Eens M. Impacts of rising temperatures and water acidification on the oxidative status and immune system of aquatic ectothermic vertebrates: A meta-analysis. Sci Total Environ. 2023; 868: 161580. https://doi.org/10.1016/j.scitotenv.2023.161580 PMID: 36646226
23. Fox RJ, Donelson JM, Schunter C, Ravasi T, Gaitán-Espitia JD. Beyond buying time: the role of plasticity in phenotypic adaptation to rapid environmental change. Phil Trans Roy Soc B. 2019; 374 (1768): 20180174. https://doi.org/10.1098/rstb.2018.0174 PMID: 30966962

24. Angilletta MJ. Thermal adaptation: A theoretical and empirical synthesis. Oxford: Oxford University Press; 2009.

25. Donelson JM, Munday PL, McCormick M, Nilsson GE. Acclimation to predicted ocean warming through developmental plasticity in a tropical reef fish. Glob Chang Biol. 2011; 17(4): 1712–1719.

26. Donelson JM. Development in a warm future ocean may enhance performance in some species. J Exp Mar Biol Ecol. 2015; 472: 119–125.

27. Veilleux HD, Ryu T, Donelson JM, Ravasi T, Munday PL. Molecular response to extreme summer temperatures differs between two genetically differentiated populations of a coral reef fish. Front Mar Sci. 2018; 5: 349.

28. Bernal MA, Donelson JM, Veilleux HD, Ryu T, Munday PL, Ravasi T. Phenotypic and molecular consequences of stepwise temperature increase across generations in a coral reef fish. Mol Ecol. 2018; 27(22): 4516–4528. https://doi.org/10.1111/mec.14884 PMID: 30267545

29. Moore B, Jolly J, Izumiyama M, Kawai E, Ryu T, Ravasi T. Clownfish larvae exhibit faster growth, higher metabolic rates and altered gene expression under future ocean warming. Sci Total Environ. 2023; 873: 162296. https://doi.org/10.1016/j.scitotenv.2023.162296 PMID: 36801344

30. Ryu T, Veilleux HD, Donelson JM, Munday PL, Ravasi T. The epigenetic landscape of transgenerational acclimation to ocean warming. Nat Clim Chang. 2018; 8(6): 504–509.

31. Ryu T, Veilleux HD, Munday PL, Jung I, Donelson JM, Ravasi T. An epigenetic signature for within-generational plasticity of a reef fish to ocean warming. Front Mar Sci. 2020; 7: 284.

32. Bernal MA, Schunter C, Lehmann R, Lightfoot DJ, Allan BJM, Veilleux HD, et al. Species-specific molecular responses of wild coral reef fishes during a marine heatwave. Sci Adv. 2020; 6(12): eaay3423. https://doi.org/10.1126/sciadv.aay3423 PMID: 32206711

33. Wang S, Lau K, Lai KP, Zhang J-W, Tse AC-K, Li J-W, et al. Hypoxia causes transgenerational impairments in reproduction of fish. Nat Comm. 2016; 7: 12114. https://doi.org/10.1038/ncomms12114 PMID: 27373813

34. Lehmann R, Lightfoot DJ, Schunter C, Michell CT, Ohyanagi H, Mineta K, et al. Finding Nemo's Genes: A chromosome-scale reference assembly of the genome of the orange clownfish *Amphiprion percula*. Mol Ecol Resour. 2019; 19(3): 570–585.

35. Schunter C, Welch MJ, Nilsson GE, Rummer JL, Munday PL, Ravasi T. An interplay between plasticity and parental phenotype determines impacts of ocean acidification on a reef fish. Nat Ecol Evol. 2018; 2: 334–342. https://doi.org/10.1038/s41559-017-0428-8 PMID: 29255298

36. Kang J, Nagelkerken I, Rummer JL, Rodolfo-Metalpa R, Munday PL, Ravasi T, et al. Rapid evolution fuels transcriptional plasticity to ocean acidification. Glob Chang Biol. 2022; 28(9): 3007–3022. https://doi.org/10.1111/gcb.16119 PMID: 35238117

37. Ross PM, Scanes E, Byrne M, Ainsworth T, Donelson JM, Foo SA, et al. Surviving the Anthropocene: The resilience of marine organisms to climate change. Oceanogr Mar Biol Ann Rev. 2023; 61: Forthcoming.

38. Crozier LG, Hutchings JA. Plastic and evolutionary responses to climate change in fish. Evol Appl. 2014; 7: 68–87. https://doi.org/10.1111/eva.12135 PMID: 24454549

39. Munday PL. Transgenerational acclimation of fishes to climate change and ocean acidification. F1000Prime Rep. 2014; 6: 99. https://doi.org/10.12703/P6-99 PMID: 25580253

40. Donelson JM, Munday PL, McCormick MI, Pitcher CR. Rapid transgenerational acclimation of a tropical reef fish to climate change. Nat Clim Chang. 2012; 2(1): 30–32.

41. McMahon SJ, Donelson JM, Munday PL. Food ration does not influence the effect of elevated CO_2 on antipredator behaviour of a reef fish. Mar Ecol Progr Ser. 2018; 586: 155–166.

42. Barton BA. Stress in fishes: A diversity of responses with particular reference to changes in circulating corticosteroids. Integr Comp Biol. 2002; 42: 517–525. https://doi.org/10.1093/icb/42.3.517 PMID: 21708747

43. Wendelaar Bonga SE. The stress response in fish. Physiol Rev. 1997; 77(3): 591–625. https://doi.org/10.1152/physrev.1997.77.3.591 PMID: 9234959

44. Mommsen TP, Vijayan MM, Moon TW. Cortisol in teleosts: dynamics, mechanisms of action, and metabolic regulation. Rev Fish Biol Fish. 1999; 9: 211–268.

45. Johansen JL, Nadler LE, Habary A, Bowden AJ, Rummer JL. Thermal acclimation of tropical reef fishes to global heat waves. eLife. 2021; 10: e59162.

46. Wedemeyer GA, Barton BA, McLeay DJ. Stress and acclimation. In: Schreck CB, Moyle PB, editors. Methods for fish biology. Bethesda: American Fisheries Society; 1990. pp. 451–489.

47. Chrousos GP. Stressors, stress, and neuroendocrine integration of the adaptive response. Ann NY Acad Sci. 1998; 85(1): 311–335.

48. Barton BA, Iwama GK. Physiological changes in fish from stress in aquaculture with emphasis on the response and effects of corticosteroids. Ann Rev Fish Dis. 1991; 1: 13–26.

49. Sampaio E, Santos C, Rosa IC, Ferreira V, Pörtner H-O, Duarte CM, et al. Impacts of hypoxic events surpass those of future ocean warming and acidification. Nat Ecol Evol. 2021; 5: 311–321. https://doi.org/10.1038/s41559-020-01370-3 PMID: 33432134

50. Rummer JL, Illing B. Coral reef fishes in a multi-stressor world. In: Fangue NA, Farrell AP, Cooke SJ, editors. Fish Physiology. 2022; 39B: 325–391.

51. Wong BBM, Candolin U. Behavioral responses to changing environments. Behav Ecol. 2015; 26(3): 665–673.

52. Allan BJ, Lefrançois C, McCormick MI. The effect of climate change on the escape kinematics and performance of fishes: implications for future predator–prey interactions. Conserv Phys. 2019; 7(1): coz078. https://doi.org/10.1093/conphys/coz078 PMID: 31723432

53. Nagelkerken I, Doney SC, Munday PL. Consequences of anthropogenic changes in the sensory landscape of marine animals. Oceanogr Mar Biol Ann Rev. 2018; 57: 229–264.

54. Tigert LR, Porteus CS. Invited review—the effects of anthropogenic abiotic stressors on the sensory systems of fishes. Comp Biochem Physiol Part A Mol Integr Phys. 2023; 277: 111366. https://doi.org/10.1016/j.cbpa.2022.111366 PMID: 36586568

55. Nilsson GE, Dixson DL, Domenici P, McCormick MI, Sørensen C, Watson SA, et al. Near-future carbon dioxide levels alter fish behaviour by interfering with neurotransmitter function. Nat Clim Chang. 2012; 2(3): 201–204.

56. Williams CR, Dittman AH, McElhany P, Busch S, Maher MT, Bammler Tk, et al. Elevated CO_2 impairs olfactory-mediated neural and behavioral responses and gene expression in ocean-phase coho salmon (*Oncorhynchus kisutch*). Glob Chang Biol. 2019; 25: 963–977.

57. Hu N, Bourdeau PE, Harlos C, Liu Y, Hollander J. Meta-analysis reveals variance in tolerance to climate change across marine trophic levels. Sci Total Environ. 2022; 827: 154244. https://doi.org/10.1016/j.scitotenv.2022.154244 PMID: 35245550

58. Krause J, Ruxton GD. Living in groups. Oxford: Oxford University Press; 2002.

59. Domenici P, Steffensen JF, Marras S. The effect of hypoxia on fish schooling. Phil Trans Roy Soc B: Biol Sci. 2017; 372(1727): 20160236.

60. Mitchell A, Booth DJ, Nagelkerken I. Ocean warming and acidification degrade shoaling performance and lateralization of novel tropical–temperate fish shoals. Glob Chang Biol. 2022; 28(4): 1388–1401. https://doi.org/10.1111/gcb.16022 PMID: 34918444

61. Nadler LE, Killen SS, McCormick MI, Watson SA, Munday PL. Effect of elevated carbon dioxide on shoal familiarity and metabolism in a coral reef fish. Conserv Phys. 2016; 4(1): cow052.

62. Domenici P, Allan B, McCormick MI, Munday PL. Elevated carbon dioxide affects behavioural lateralization in a coral reef fish. Biol Lett. 2012; 8(1): 78–81. https://doi.org/10.1098/rsbl.2011.0591 PMID: 21849307

63. Watson SA, Allan BJ, McQueen DE, Nicol S, Parsons D, Pether SM, et al. Ocean warming has a greater effect than acidification on the early life history development and swimming performance of a large circumglobal pelagic fish. Glob Chang Biol. 2018; 24(9): 4368–4385. https://doi.org/10.1111/gcb.14290 PMID: 29790239

64. Domenici P, Steffensen JF, Batty RS. The effect of progressive hypoxia on swimming activity and schooling in Atlantic herring. J Fish Biol. 2000; 57(6): 1526–1538.

65. Jarrold MD, Humphrey C, McCormick MI, Munday PL. Diel CO_2 cycles reduce severity of behavioural abnormalities in coral reef fish under ocean acidification. Sci Rep. 2017; 7(1): 10153.

66. Goldenberg SU, Nagelkerken I, Marangon E, Bonnet A, Ferreira CM, Connell SD. Ecological complexity buffers the impacts of future climate on marine consumers. Nat Clim Chang. 2019; 8(3): 229–233.

67. Nagelkerken I, Goldenberg SU, Ferreira CM, Russell BD, Connell SD. Species interactions drive fish biodiversity loss in a high-CO_2 world. Curr Biol. 2017; 27(14), 2177–2184.

68. Coni E, Nagelkerken I, Ferreira CM, Connell SD, Booth DJ. Ocean acidification may slow the pace of tropicalization of temperate fish communities. Nat Clim Chang. 2021; 11: 249–256.

69. Rahman T, Candolin U. Linking animal behaviour to ecosystem change in disturbed environments. Front Ecol Evol. 2022; 10: 893453.

70. Chaudhary C, Richardson AJ, Schoeman DS, Costello MJ. Global warming is causing a more pronounced dip in marine species richness around the equator. Proc Nat Acad Sci USA. 2021; 118: e2015094118. https://doi.org/10.1073/pnas.2015094118 PMID: 33876750

71. Snucins EJ, Gunn JM. Coping with a warm environment: Behavioral thermoregulation by Lake Trout. Trans Am Fish Soc. 1995; 124: 118–123.

72. Muñoz MM. The Bogert effect, a factor in evolution. Evolution 2021; 76: 49–66. https://doi.org/10.1111/evo.14388 PMID: 34676550

73. Rogers LA, Dougherty AB. Effects of climate and demography on reproductive phenology of a harvested marine fish population. Glob Chang Biol. 2019; 25: 708–720. https://doi.org/10.1111/gcb.14483 PMID: 30430699

74. Pankhurst NW, Munday PL. Effects of climate change on fish reproduction and early life history stages. Mar Freshw Res. 2011; 62: 1015–1026.

75. Woods T, Kaz A, Giam X. Phenology in freshwaters: a review and recommendations for future research. Ecography. 2022: e05564.

76. Asch RG, Stock CA, Sarmiento JL. Climate change impacts on mismatches between phytoplankton blooms and fish spawning phenology. Glob Chang Biol. 2019; 25: 2544–2559. https://doi.org/10.1111/gcb.14650 PMID: 31152499

77. Bonhommeau S, Chassot E, Planque B, Rivot E, Knap AH, Le Pape O. Impact of climate on the eel populations of the Northern Hemisphere. Mar Ecol Prog Ser. 2008; 373: 71–80.

78. Hoffmann AA, Sgro CM. Climate change and evolutionary adaptation. Nature. 2011; 470: 479–485. https://doi.org/10.1038/nature09670 PMID: 21350480

79. Thurman LL, Stein BA, Beever EA, Foden W, Geange SR, Green N, et al. Persist in place or shift in space? Evaluating the adaptive capacity of species to climate change. Front Ecol Environ. 2020; 18: 520–528.

80. Audzijonyte A, Richards SA, Stuart-Smith RD, Pecl G, Edgar GJ, Barrett NS, et al. Fish body sizes change with temperature but not all species shrink with warming. Nat Ecol Evol. 2020; 4: 809–814. https://doi.org/10.1038/s41559-020-1171-0 PMID: 32251381

81. Ruiz-Navarro A, Gillingham PK, Britton JR. Shifts in the climate space of temperate cyprinid fishes due to climate change are coupled with altered body sizes and growth rates. Glob Chang Biol. 2016; 22: 3221–3232. https://doi.org/10.1111/gcb.13230 PMID: 26824727

82. Rijnsdorp AD, Peck MA, Engelhard GH, Möllmann C, Pinnegar JK. Resolving the effect of climate change on fish populations. ICES J Mar Sci. 2009; 66: 1570–1583.

83. Koenigstein S, Dahlke FT, Stiasny MH, Storch D, Clemmesen C, Portner HO. Forecasting future recruitment success for Atlantic cod in the warming and acidifying Barents Sea. Glob Chang Biol. 2018; 24(1): 526–535. https://doi.org/10.1111/gcb.13848 PMID: 28755499

84. Pollock MS, Clarke LMJ, Dubé MG. The effects of hypoxia on fishes: from ecological relevance to physiological effects. Environ Rev. 2007; 15: 1–14.

85. Whalen MA, Whippo RD, Stachowicz JJ, York PH, Aiello E, Alcoverro T, et al. Climate drives the geography of marine consumption by changing predator communities. Proc Nat Acad Sci USA. 2020; 117 (45): 28160–28166. https://doi.org/10.1073/pnas.2005255117 PMID: 33106409

86. Hammerstein P, Selten R. Game theory and evolutionary biology. In: Aumann R, Hart S, editors. Handbook of game theory with economic applications. Amsterdam: North-Holland; 1994. Volume 2, pp. 929–993.

87. Bshary R, Oliveira RF. Cooperation in animals: toward a game theory within the framework of social competence. Curr Opin Behav Sci. 2015; 3: 31–37.

88. Buñuel X, Alcoverro T, Romero J, Arthur R, Ruiz JM, Pérez M, et al. Warming intensifies the interaction between the temperate seagrass *Posidonia oceanica* and its dominant fish herbivore *Sarpa salpa*. Mar Env Res. 2021; 165: 105237.

89. Allan BJ, Domenici P, McCormick MI, Watson SA, Munday PL. Elevated CO_2 affects predator-prey interactions through altered performance. PLoS One. 2014; 8(3): e58520.

90. Allan BJ, Domenici P, Munday PL, McCormick MI. Feeling the heat: the effect of acute temperature changes on predator–prey interactions in coral reef fish. Conserv Physiol. 2015; 3(1): cov011. https://doi.org/10.1093/conphys/cov011 PMID: 27293696

91. McCormick MI, Watson SA, Munday PL. Ocean acidification reverses competition for space as habitats degrade. Sci Rep. 2013; 3(1): 3280. https://doi.org/10.1038/srep03280 PMID: 24263692

92. Matis PA, Donelson JM, Bush S, Fox RJ, Booth DJ. Temperature influences habitat preference of coral reef fishes: Will generalists become more specialised in a warming ocean? Glob Chang Biol. 2018; 24(7): 3158–3169. https://doi.org/10.1111/gcb.14166 PMID: 29658157

93. Freitas C, Villegas-Ríos D, Moland E, Olsen EM. Sea temperature effects on depth use and habitat selection in a marine fish community. J Anim Ecol. 2021; 90(7): 1787–1800. https://doi.org/10.1111/1365-2656.13497 PMID: 33844859

94. Nagelkerken I, Goldenberg SU, Ferreira CM, Connell SD. Trophic pyramids reorganize when food web architecture fails to adjust to ocean change. Science. 2020; 369: 829–832. https://doi.org/10.1126/science.aax0621 PMID: 32792395

95. Urban MC, Tewksbury JJ, Sheldon KS. On a collision course: competition and dispersal differences create no-analogue communities and cause extinctions during climate change. Proc Roy Soc B: Biol Sci. 2012; 279: 2072–2080.

96. Huey RB, Kearney MR, Krockenberger A, Holtum JAM, Jess M, Williams SE. Predicting organismal vulnerability to climate warming: roles of behaviour, physiology and adaptation. Phil Trans R Soc B: Biol Sci. 2012; 367: 1665–1679.

97. Booth DJ, Poulos DE, Poole J, Feary DA. Growth and temperature relationships for juvenile fish species in seagrass beds: implications of climate change. J Fish Biol. 2014; 84(1): 231–236. https://doi.org/10.1111/jfb.12255 PMID: 24383807

98. Kingsbury KM, Gillanders BM, Booth DJ, Nagelkerken I. Trophic niche segregation allows range-extending coral reef fishes to co-exist with temperate species under climate change. Glob Chang Biol. 2020; 26(2): 721–733. https://doi.org/10.1111/gcb.14898 PMID: 31846164

99. Watson AS, Hickford MJH, Schiel DR. Interacting effects of density and temperature on fish growth rates in freshwater protected populations. Proc Roy Soc. B. 2022; 289: 20211982. https://doi.org/10.1098/rspb.2021.1982 PMID: 35042421

100. Sánchez-Hernández J, Hayden B, Harrod C, Kahilainen KK, et al. Population niche breadth and individual trophic specialisation of fish along a climate-productivity gradient. Rev Fish Biol Fish. 2021; 31: 1025–1043.

101. Stuart-Smith RD, Mellin C, Bates AE, Edgar G. Habitat loss and range shifts contribute to ecological generalization amongst reef fishes. Nat Ecol Evol. 2021; 5: 656–662.

102. LeFeuvre MC, Dempster T, Shelley JJ, Davis AM, Swearer SE. Range restriction leads to narrower ecological niches and greater extinction risk in Australian freshwater fish. Biodiv Conserv. 2021; 30: 2955–2976.

103. Pratchett MS, Thompson CA, Hoey AS, Cowman PF, Wilson SK. Effects of coral bleaching and coral loss on the structure and function of reef fish assemblages. In: van Oppen M, Lough J, editors. Coral bleaching–patterns, processes, causes and consequences. Ecological Studies. vol 233. Cham: Springer;2018. pp. 265–293.

104. Froehlich CYM, Klanten OS, Hing ML, Dowton M, Wong MYL. Uneven declines between corals and cryptobenthic fish symbionts from multiple disturbances. Sci Rep. 2021; 11: 16420. https://doi.org/10.1038/s41598-021-95778-x PMID: 34385506

105. Narvaez P, Morais RA, Hutson KS, McCormick MI, Grutter AS. Habitat degradation drives increased gnathiid isopod ectoparasite infection rate on juvenile but not adult fish. Coral Reefs. 2021; 40: 1867–1877.

106. Artim JM, Nicholson MD, Hendrick GC, Brandt M, Smith TB, Sikkel PC. Abundance of a cryptic generalist parasite reflects degradation of an ecosystem. Ecosphere. 2020; 11: e03268.

107. Paula JR, Repolho T, Pegado MR, Thörnqvist P-O, Bispo R, Winberg S, et al. Neurobiological and behavioural responses of cleaning mutualisms to ocean warming and acidification. Sci Rep. 2019; 9: 12728. https://doi.org/10.1038/s41598-019-49086-0 PMID: 31484945

108. Paula JR, Repolho T, Grutter AS, Rosa R. Access to cleaning services alters fish physiology under parasite infection and ocean acidification. Front Physiol. 2022; 13: 859556. https://doi.org/10.3389/fphys.2022.859556 PMID: 35755439

109. Paula JR, Otjacques E, Hildebrandt C, Grutter AS, Rosa R. Ocean acidification does not affect fish ectoparasite survival. Oceans. 2020; 1: 27–33.

110. Abdel-Tawwab M, Monier MN, Hoseinifar SH, Faggio C. Fish response to hypoxia stress: growth, physiological, and immunological biomarkers. Fish Physiol Biochem. 2019; 45: 997–1013. https://doi.org/10.1007/s10695-019-00614-9 PMID: 30715663

111. Nagelkerken I, Pitt KA, Rutte MD, Geertsma RC. Ocean acidification alters fish–jellyfish symbiosis. Proc Roy Soc B. 2016; 283: 20161146. https://doi.org/10.1098/rspb.2016.1146 PMID: 27358374

112. Norin T, Mills SC, Crespel A, Cortese D, Killen SS, Beldade R. Anemone bleaching increases the metabolic demands of symbiont anemonefish. Proc Roy Soc B. 2018; 285: 20180282. https://doi.org/10.1098/rspb.2018.0282 PMID: 29643214

113. Harvell D. Ocean outbreak—Confronting the rising tide of marine disease. Oakland: University of California Press; 2021.

114. Bashevkin SM, Dibble CD, Dunn RP, Hollarsmith JA, Ng G, Satterthwaite EV, et al. Larval dispersal in a changing ocean with an emphasis on upwelling regions. Ecosphere. 2020; 11(1): e03015.

115. O'Connor MI, Bruno JF, Gaines SD, Halpern BS, Lester SE, Kinlan BP, et al. Temperature control of larval dispersal and the implications for marine ecology, evolution, and conservation. Proc Nat Acad Sci USA. 2007; 104: 1266–1271. https://doi.org/10.1073/pnas.0603422104 PMID: 17213327

116. Perry AL, Low PJ, Ellis JR, Reynolds JD. Climate change and distribution shifts in marine fishes. Science. 2005; 308: 1912–1915. https://doi.org/10.1126/science.1111322 PMID: 15890845

117. McLean M, Mouillot D, Maureaud AA, Hattab T, MacNeil MA, Goberville E, et al. Disentangling tropicalization and deborealization in marine ecosystems under climate change. Curr Biol. 2021; 31: 4817–4823. https://doi.org/10.1016/j.cub.2021.08.034 PMID: 34499852

118. Bates AE, Barrett NS, Stuart-Smith RD, Holbrook NJ, Thompson PA, Edgar GJ. Resilience and signatures of tropicalization in protected reef fish communities. Nat Clim Chan. 2014; 4: 62–67.

119. Smith SM, Malcolm HA, Marzinelli EM, Schultz AL, Steinberg PD, Vergés A. Tropicalisation and kelp loss shift trophic composition and lead to more winners than losers in fish communities. Glob Chang Biol. 2021; 27(11): 2537–2548.

120. Longo GO, Hay ME, Ferreira CEL, Floeter SR. Trophic interactions across 61 degrees of latitude in the Western Atlantic. Glob Ecol Biogeogr. 2019; 28: 107–117.

121. Holland MM, Smith JA, Everett JD, Vergés A, Suthers IM. Latitudinal patterns in trophic structure of temperate reef-associated fishes and predicted consequences of climate change. Fish Fish. 2020; 21: 1092–1108.

122. Coni E, Booth DJ, Ferreira CM, Nagelkerken I. Behavioural generalism facilitates co-existence of tropical and temperate fishes under climate change. J Anim Ecol. 2022; 91: 86–100.

123. Monaco CJ, Bradshaw CJA, Booth DJ, Gillanders BM, Schoeman DS, Nagelkerken I Dietary generalism accelerates arrival and persistence of coral-reef fishes in their novel ranges under climate change. Glob Chang Biol. 2020; 26: 5564–5573.

124. Fossheim M, Primicerio R, Johannesen E, Ingvaldsen RB, Aschan MM, Dolgov AV. Recent warming leads to a rapid borealization of fish communities in the Arctic. Nat Clim Chang. 2015; 5(7): 673–677.

125. Frainer A, Primicerio R, Kortsch S, Aune M, Dolgov AV, Fossheim M, et al. Climate-driven changes in functional biogeography of Arctic marine fish communities. Proc Nat Acad Sci USA. 2017; 114(46): 12202–12207. https://doi.org/10.1073/pnas.1706080114 PMID: 29087943

126. Vergés A, Steinberg PD, Hay ME, Poore AGB, Campbell AH, Ballesteros E, et al. The tropicalization of temperate marine ecosystems: climate-mediated changes in herbivory and community phase shifts. Proc Roy Soc B:Biol Sci. 2014a; 281: 20140846.

127. Vergés A, Tomas F, Cebrian E, Ballesteros E, Kizilkaya Z, Dendrinos P, et al. Tropical rabbitfish and the deforestation of a warming temperate sea. J Ecol. 2014b; 102: 1518–1527.

128. Bennett S, Wernberg T, Harvey ES, Santana-Garcon J, Saunders BJ. Tropical herbivores provide resilience to a climate-mediated phase shift on temperate reefs. Ecol Lett. 2015; 18: 714–723. https://doi.org/10.1111/ele.12450 PMID: 25994785

129. Vergés A, Doropoulos C, Malcolm HA, Skye M, Garcia-Piza M, Marzinelli EM, et al. Long-term empirical evidence of ocean warming leading to tropicalization of fish communities, increased herbivory and loss of kelp. Proc Nat Acad Sci USA. 2016; 113(48): 13791–13796. https://doi.org/10.1073/pnas.1610725113 PMID: 27849585

130. Cattano C, Agostini S, Harvey BP, Wada S, Quattrocchi F, Turco G, et al. Changes in fish communities due to benthic habitat shifts under ocean acidification conditions. Sci Total Environ. 2020; 725: 138501. https://doi.org/10.1016/j.scitotenv.2020.138501 PMID: 32298893

131. Leriorato JC, Nakamura Y. Unpredictable extreme cold events: A threat to range-shifting tropical reef fishes in temperate waters. Mar Biol. 2019; 166(8): 110.

132. Pessarrodona A, Vergés A, Bosch NE, Bell S, Smith S, Sgarlatta MP, et al. Tropicalization unlocks novel trophic pathways and enhances secondary productivity in temperate reefs. Funct Ecol. 2022; 36: 659–673.

133. Zarco-Perello S, Langlois TJ, Holmes T, Vanderklift MA, Wernberg T. Overwintering tropical herbivores accelerate detritus production on temperate reefs. Proc Roy Soc B. 2019; 286: 20192046. https://doi.org/10.1098/rspb.2019.2046 PMID: 31744442

134. Escalas A, Avouac A, Villeger S, Escalas A, Avouac A, Belmaker J, et al. An invasive herbivorous fish (*Siganus rivulatus*) influences both benthic and planktonic microbes through defecation and nutrient excretion. Sci Total Environ. 2022; 838: 56207.

135. Knight NS, Guichard F, Altieri AH. A global meta-analysis of temperature effects on marine fishes' digestion across trophic groups. Glob Ecol Biogeogr. 2021; 30: 795–810.

136. Pecuchet L, Jørgensen LL, Dolgov AV, Eriksen E, Husson B, Skern-Mauritzen M, et al. Spatio-temporal turnover and drivers of bentho-demersal community and food web structure in a high-latitude marine ecosystem. Divers Distrib. 2022; 28(12): 2503–2520.

137. Goldenberg SU, Nagelkerken I, Ferreira CM, Ullah H, Connell SD. Boosted food web productivity through ocean acidification collapses under warming. Glob Chang Biol. 2017; 23: 4177–4184. https://doi.org/10.1111/gcb.13699 PMID: 28447365

138. Roman MR, Brandt SB, Houde ED, Pierson JJ. Interactive effects of hypoxia and temperature on coastal pelagic zooplankton and fish. Front Mar Sci. 2019; 6: 139.

139. Mellin C, Mouillot D, Kulbicki M, McClanahan TR, Vigliola L, Bradshaw CJA, et al. Humans and seasonal climate variability threaten large-bodied coral reef fish with small ranges. Nat Comm. 2016; 7: 10491. https://doi.org/10.1038/ncomms10491 PMID: 26839155

140. Cooke R, Gearty W, Chapman ASA, Dunic J, Edgar GJ, Lefcheck JS, et al. Anthropogenic disruptions to longstanding patterns of trophic-size structure in vertebrates. Nat Ecol Evol. 2022; 6: 684–692. https://doi.org/10.1038/s41559-022-01726-x PMID: 35449460

141. Edgar GJ, Alexander TJ, Lefcheck JS, Bates AE, Kininmonth SJ, Thomson RJ, et al. Abundance and local-scale processes contribute to multi-phyla gradients in global marine diversity. Sci Adv. 2017; 3: e1700419. https://doi.org/10.1126/sciadv.1700419 PMID: 29057321

142. Chaudhary C, Saeedi H, Costello MJ. Bimodality of latitudinal gradients in marine species richness. Trends Ecol Evol. 2016; 31: 670–676. https://doi.org/10.1016/j.tree.2016.06.001 PMID: 27372733

143. Stuart-Smith RD, Edgar GJ, Bates AE. Thermal limits to the geographic distributions of shallow-water marine species. Nat Ecol Evol. 2017; 1: 1846–1852. https://doi.org/10.1038/s41559-017-0353-x PMID: 29062125

144. Barneche DR, Rezende EL, Parravicini V, Maire E, Edgar GJ, Stuart-Smith RD, et al. Body size, reef area and temperature predict global reef-fish species richness across spatial scales. Glob Ecol Biogeogr. 2019; 28: 315–327.

145. Siqueira AC, Morais RA, Bellwood DR, Cowman PF. Planktivores as trophic drivers of global coral reef fish diversity patterns. Proc Nat Acad Sci USA. 2021; 118: e2019404118. https://doi.org/10.1073/pnas.2019404118 PMID: 33593939

146. Edgar GJ, Cooper A, Baker SC, Barker W, Barrett NS, Becerro MA, et al. Reef Life Survey: Establishing the ecological basis for conservation of shallow marine life. Biol Conserv. 2020; 252: 108855.

147. Edgar GJ, Bates AE, Bird TJ, Jones AH, Kininmonth S, Stuart-Smith RD, et al. New approaches to marine conservation through the scaling up of ecological data. Ann Rev Mar Sci. 2016; 8:435–461. https://doi.org/10.1146/annurev-marine-122414-033921 PMID: 26253270

148. McLean M, Mouillot D, Lindegren M, Villéger S, Engelhard G, Murgier J, et al. Fish communities diverge in species but converge in traits over three decades of warming. Glob Chang Biol. 2019b; 25: 3972–3984. https://doi.org/10.1111/gcb.14785 PMID: 31376310

149. Baptista J, Martinho F, Nyitrai D, Pardal MA, Dolbeth M. Long-term functional changes in an estuarine fish assemblage. Mar Poll Bull. 2015; 97: 125–134.

150. Daufresne M, Boet P. Climate change impacts on structure and diversity of fish communities in rivers. Glob Chang Biol. 2007; 13: 2467–2478.

151. Teichert N, Pasquaud S, Borja A, Chust G, Uriarte A, Lepage M. Living under stressful conditions: Fish life history strategies across environmental gradients in estuaries. Estuar Coast Shelf Sci. 2017; 188: 18–26.

152. Scherer L, Boom HA, Barbarossa V, van Bodegom PM. Climate change threats to the global functional diversity of freshwater fish. Glob Chang Biol. 2023; 29(13): 3781–3793. https://doi.org/10.1111/gcb.16723 PMID: 37070402

153. McLean M, Auber A, Graham NAJ, Houk P, Villéger S, Violle C, et al. Trait structure and redundancy determine sensitivity to disturbance in marine fish communities. Glob Chang Biol. 2019a; 25: 3424–3437. https://doi.org/10.1111/gcb.14662 PMID: 31006156

154. Diaz RJ, Rosenberg R. Spreading dead zones and consequences for marine ecosystems. Science. 2008; 321: 926–929. https://doi.org/10.1126/science.1156401 PMID: 18703733

155. Galappaththi EK, Susarla VB, Loutet SJT, Ichien ST, Hyman AA, Ford JD. Climate change adaptation in fisheries. Fish Fish. 2022; 23: 4–21.

156. Cheung WWL, Sarmiento JL, Dunne J, Frolicher TL, Lam VWY, Deng Palomares ML, et al. Shrinking of fishes exacerbates impacts of global ocean changes on marine ecosystems. Nat Clim Chang. 2013; 3: 254–258.

157. Cheung WWL, Lam VWY, Sarmiento JL, Kearney K, Watson R, Pauly D. Projecting global marine biodiversity impacts under climate change scenarios. Fish Fish. 2009; 10(3): 235–51.

158. Pinsky ML, Reygondeau G, Caddell R, Palacios-Abrantes J, Spijkers J, Cheung WWL. Preparing ocean governance for species on the move. Science 2018; 360: 1189–1191. https://doi.org/10.1126/science.aat2360 PMID: 29903965

159. Cheung WWL, Reygondeau G, Frölicher TL. Large benefits to marine fisheries of meeting the 1.5 ˚C global warming target. Science. 2016; 354(6319): 1591–1594.

160. Golden C, Allison E, Cheung W, Dey M, Halpern B, McCauley D, et al. Nutrition: Fall in fish catch threatens human health. Nature. 2016; 534: 317–320. https://doi.org/10.1038/534317a PMID: 27306172

161. Hicks CC, Cohen PJ, Graham NAJ, Nash KL, Allison EH, D'Lima C, et al. Harnessing global fisheries to tackle micronutrient deficiencies. Nature. 2019; 574: 95–98. https://doi.org/10.1038/s41586-019-1592-6 PMID: 31554969

162. Mellin C, Hicks C, Fordham DA, Golden C, Kjellevold M, MacNeil MA, et al. Safeguarding nutrients from coral reefs under climate change. Nat Ecol Evol. 2022; 6: 1808–1817. https://doi.org/10.1038/s41559-022-01878-w PMID: 36192542

163. Robinson JPW, Maire E, Bodin N, Hempson TN, Graham NAJ, Wilson SK, et al. Climate-induced increases in micronutrient availability for coral reef fisheries. One Earth. 2022; 5: 98–108. https://doi.org/10.1016/j.oneear.2021.12.005 PMID: 35128392

164. Coleman MA, Butcherine P, Kelaher BP, Broadhurst MK, March DT, Provost EJ, et al. Climate change does not affect the seafood quality of a commonly targeted fish. Glob Chang Biol. 2019; 25(2): 699–707. https://doi.org/10.1111/gcb.14513 PMID: 30414338

165. Maire E, Graham NAJ, MacNeil MA, Lam VWY, Robinson JPW, Cheung WWL, et al. Micronutrient supply from global marine fisheries under climate change and overfishing. Curr Biol. 2021; 31: 4132–4138 https://doi.org/10.1016/j.cub.2021.06.067 PMID: 34289388

166. Grorud-Colvert K, Sullivan-Stack J, Roberts C, Constant V, Costa BHe, Pike EP, et al. The MPA Guide: A framework to achieve global goals for the ocean. Science. 2021; 373: eabf0861. https://doi.org/10.1126/science.abf0861 PMID: 34516798

167. Edgar GJ Russ GR, Babcock RC. Marine protected areas. In: Connell S, Gillanders BM, editors. Marine Ecology. South Melbourne: Oxford University Press; 2007. pp. 533–555.

168. Cahill AE, Aiello-Lammens ME, Fisher-Reid MC, Hua X, Karanewsky CJ, Yeong Ryu H, et al. How does climate change cause extinction? Proc Roy Soc B: Biol Sci. 2013; 280: 20121890.

169. Torio DD, Chmura GL. Impacts of sea level rise on marsh as fish habitat. Estuaries Coasts. 2015; 38: 1288–1303.

170. Nyboer EA, Lin H-Y, Bennett JR, Gabriel J, Twardek W, Chhor AD, et al. Global assessment of marine and freshwater recreational fish reveals a mismatch in climate change vulnerability and conservation effort. Glob Chang Biol. 2021; 27: 4799–4824.

171. Donovan MK, Burkepile DE, Kratochwill C, Shlesinger T, Sully S, Oliver TA, et al. Local conditions magnify coral loss after marine heatwaves. Science. 2021; 372: 977–980. https://doi.org/10.1126/science.abd9464 PMID: 34045353

172. Fredston-Hermann A, Gaines SD, Halpern BS. Biogeographic constraints to marine conservation in a changing climate. Ann NY Acad Sci. 2018; 1429: 5–17. https://doi.org/10.1111/nyas.13597 PMID: 29411385

173. Duarte CM, Agusti S, Barbier E, Britten GL, Castilla JC, Gattuso J-P, et al. Rebuilding marine life. Nature. 2020; 580: 39–51. https://doi.org/10.1038/s41586-020-2146-7 PMID: 32238939

174. Abelson A, Reed DC, Edgar GJ, Smith CS, Kendrick GA, Orth RJ, et al. Challenges for restoration of coastal marine ecosystems in the Anthropocene. Front Mar Sci. 2020; 7: 544105.

175. Keller BD, Gleason DF, McLeod E, Woodley CM, Airamé S, Causey BD, et al. Climate change, coral reef ecosystems, and management options for marine protected areas. Environ Manage. 2009; 44: 1069–1088. https://doi.org/10.1007/s00267-009-9346-0 PMID: 19636605

176. Gallo ND, Levin LA. Fish ecology and evolution in the World's oxygen minimum zones and implications of ocean deoxygenation. Adv Mar Biol. 2016; 74: 117–198. https://doi.org/10.1016/bs.amb.2016.04.001 PMID: 27573051

177. Toy JA, Kroeker KJ, Logan CA, Takeshita Y, Longo GC, Bernardi G. Upwelling-level acidification and pH/pCO_2 variability moderate effects of ocean acidification on brain gene expression in the temperate surfperch, *Embiotoca jacksoni*. Mol Ecol. 2022; 31: 4707–4725.

178. Beaugrand G, Kirby RR. How do marine pelagic species respond to climate change? Theories and observations. Ann Rev Mar Sci. 2018; 10(1): 169–197. https://doi.org/10.1146/annurev-marine-121916-063304 PMID: 29298137

179. Parmesan C, Yohe G. A globally coherent fingerprint of climate change impacts across natural systems. Nature. 2003; 421(6918): 37–42. https://doi.org/10.1038/nature01286 PMID: 12511946

180. Waldock C, Stuart-Smith RD, Albouy C, Cheung WWL, Edgar GJ, Mouillot D, et al. A quantitative review of abundance-based species distribution models. Ecography. 2022; e05694.

181. Moullec F, Barrier N, Drira S, Guilhaumon F, Hattab T, Peck MA, et al. Using species distribution models only may underestimate climate change impacts on future marine biodiversity. Ecol Modell. 2022; 464: 109826.

182. Bush A, Mokany K, Catullo R, Hoffmann A, Kellermann V, Sgrò C, et al. Incorporating evolutionary adaptation in species distribution modelling reduces projected vulnerability to climate change. Ecol Lett. 2016; 19: 1468–1478. https://doi.org/10.1111/ele.12696 PMID: 27873482

183. ECOPATH II—a software for balancing steady-state ecosystem models and calculating network characteristics. Ecol Modell. 1992; 61(3): 169–85.

184. Ullah H, Nagelkerken I, Goldenberg SU, Fordham DA. Climate change could drive marine food web collapse through altered trophic flows and cyanobacterial proliferation. PLoS Biol. 2018; 16(1): e2003446. https://doi.org/10.1371/journal.pbio.2003446 PMID: 29315309

185. du Pontavice H, Gascuel D, Reygondeau G, Stock C, Cheung WWL. Climate-induced decrease in biomass flow in marine food webs may severely affect predators and ecosystem production. Glob Chang Biol. 2021; 27: 2608–2622. https://doi.org/10.1111/gcb.15576 PMID: 33660891

186. Tekwa EW, Watson JR, Pinsky ML. Body size and food–web interactions mediate species range shifts under warming. Proc Roy Soc B: Biol Sci. 2022; 289: 20212755.

187. Albouy C, Velez L, Coll M, Colloca F, Le Loc'h F, Mouillot D, et al. From projected species distribution to food-web structure under climate change. Glob Chang Biol. 2014; 20: 730–741. https://doi.org/10.1111/gcb.12467 PMID: 24214576

188. Griffith GP, Fulton EA, Gorton R, Richardson AJ. Predicting interactions among fishing, ocean warming, and ocean acidification in a marine system with whole-ecosystem models. Conserv Biol. 2012; 26 (6): 1145–1152. https://doi.org/10.1111/j.1523-1739.2012.01937.x PMID: 23009091

189. Dortel E, Pecquerie L, Chassot E. A Dynamic Energy Budget simulation approach to investigate the eco-physiological factors behind the two-stanza growth of yellowfin tuna (*Thunnus albacares*). Ecol Modell. 2020; 437: 109297.

190. Wang W, Xu N, Zhang L, Andersen KH, Klaminder J. Anthropogenic forcing of fish boldness and its impacts on ecosystem structure. Glob Chang Biol. 2021; 27: 1239–1249.

191. Reddin CJ, Kocsis ÁT, Kiessling W. Marine invertebrate migrations trace climate change over 450 million years. Glob Ecol Biogeogr. 2020; 29: 1280–1282.

192. Avaria-Llautureo J, Venditti C, Rivadeneira MM, Inostroza-Michael O, Rivera RJ, Hernández C et al. Historical warming consistently decreased size, dispersal and speciation rate of fish. Nat Clim Chang. 2021; 11: 787–793.

193. Salvatteci R, Schneider RR, Galbraith E, Field D, Blanz T, Bauersachs T, et al. Smaller fish species in a warm and oxygen-poor Humboldt Current system. Science. 2022; 375(6576): 101–104. https://doi.org/10.1126/science.abj0270 PMID: 34990239

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