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## Climate Change Effects on Fishes

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### Introduction

Fishes comprise the most diverse group of aquatic vertebrates and are found across the world's aquatic biomes and ecosystems — in freshwater, estuaries, as well as in the ocean. With this diversity also comes an extensive array of life histories, behaviors, physiologies, and adaptations. In addition to long-term direct human perturbations on fish populations and communities, such as overfishing, habitat destruction, and aquatic pollution, indirect human stressors such as various climate change stressors are now increasingly having an impact on many fish species as well. It is predicted that climate change stressors such as warming, acidification, and hypoxia will alter fish biodiversity, change their geographic distributions, alter their fitness and performance, and create novel community structures. Due to their rich diversity, it is difficult to predict how each fish species will respond to the interplay of various climate stressors. However, fish species can often be classified into guilds, functional groups, life history strategies, etc., based on various traits. As such, some generalizable patterns may emerge on how specific (taxonomic/functional) groups of fish species might respond to current and future climate change. This bibliography covers key studies on climate change effects on (predominantly marine) fishes, through the lens of fish ecology. It assesses the current published literature in terms of various research fields in fish ecology, scaling up from cellular, individual, and population levels to higher levels of biological organization such as communities, ecosystems, and biogeographies. Such a broad bibliography might provide for a better appreciation of the complexity of studying climate change impacts on fishes, as their ecology is intertwined with that of many other species, habitats, and environmental drivers. The ecological responses of fishes at multiple levels of biological organization mediate their fitness, performance, and persistence, and generalizable insights are needed for their biodiversity conservation, and to evaluate their importance for various ecosystem services, including fisheries.

### General Overviews

Because the field of fish ecology is so broad, an extensive number of reviews exists on how various subfields of fish ecology are affected by climate change stressors. These reviews are dominated by the impacts of ocean warming and acidification, with much less published on, for example, the effect of hypoxia. In terms of ecosystems, coral reef fishes often dominate the literature, with much less known of fishes from estuarine and polar systems. Climate change effects on fish behavior and physiology have received much attention (and some controversy), with less emphasis on species interactions (although this field is on the rise). Studies on fish climate ecology in more natural environments (e.g., global-warming hot spots, volcanic CO<sub>2</sub> vents, semi-enclosed bays, and upwelling areas) where natural complexity is present at its fullest are still scarce but gaining attention. This section highlights reviews across various subfields of fish ecology. Heuer and Grosell 2014, cited under Behavior, provides an extensive review on the effects of elevated anthropogenic CO<sub>2</sub> on various physiological systems and processes, as well as on sensory systems and behavior. Pörtner and Peck 2010 reviews the effects of ocean acidification, warming, and oxygen reduction on fish physiology, and additionally evaluates how physiological changes might affect fishes at various levels of biological organization. Comte and Olden 2017 provides a global analysis comparing the thermal sensitivities of freshwater versus marine fishes. Sampaio, et al. 2021 uses a meta-analysis to specifically study the impacts of hypoxia (versus warming and acidification) on the ecology of marine species, including fishes. Another meta-analysis on fish responses to ocean acidification is provided by Cattano, et al. 2018, while Wang, et al. 2020, cited under Life Histories and Ecological Niches, is a large-scale analysis of the effects of warming on the ecology of fishes, with emphasis on life history effects. Besides understanding the direct effects of climate stressors on fishes, it is also critical to understand how fishes may avoid or adjust to climate change. Crozier and Hutchings 2014 reviews phenotypic plasticity of various ecological traits as well as genetic adaptation in fishes in response to climate change, while Vergés, et al. 2014 describes how fishes that avoid climate change by extending their ranges to cooler environment are ecologically altering recipient ecosystems. Duffy, et al. 2016 is a global analysis testing how various human and climate stressors and biodiversity might affect fish biomass. Changes in fish productivity have consequences for fisheries.

Nyboer, et al. 2021 is a global vulnerability assessment of marine and freshwater fishes to climate change, linking this to socioeconomic values and conservation efforts.

**Cattano, C., J. Claudet, P. Domenici, and M. Milazzo. 2018. Living in a high CO<sub>2</sub> world: A global meta-analysis shows multiple trait-mediated fish responses to ocean acidification. *Ecological Monographs* 88.3: 320–335.**

Meta-analysis on how ocean acidification affects multiple physiological and behavioral traits in marine fishes. Finds alterations (both negative and positive effects) in calcification, metabolism, yolk, behavior, predation risk, and foraging, but such changes were largely limited to more extreme *p*CO<sub>2</sub> elevations (300–750  $\mu$ atm). Notes that climate change effects on reproduction, development, and habitat choice of fishes are still understudied.

**Comte, L., and J. D. Olden. 2017. Climatic vulnerability of the world's freshwater and marine fishes. *Nature Climate Change* 7.10: 718–722.**

Studies the thermal tolerances of 2,960 freshwater and marine fish species. Finds that for marine systems, fishes in the tropics are most at risk, while for freshwater systems, fishes from higher northern latitudes appear most sensitive. These stark differences between biomes are stipulated to be the consequence of their different biogeographical histories.

**Crozier, L. G., and J. A. Hutchings. 2014. Plastic and evolutionary responses to climate change in fish. *Evolutionary Applications* 7.1: 68–87.**

Evaluates the degree of phenotypic responses in marine and freshwater fishes to climate change and natural climatic oscillations. Temperature, in particular, was shown to alter the timing of reproduction and migrations, age at maturity and juvenile migration, and fitness-related traits such as growth, survival, and fecundity.

**Duffy, J. E., J. S. Lefcheck, R. D. Stuart-Smith, S. A. Navarrete, and G. J. Edgar. 2016. Biodiversity enhances reef fish biomass and resistance to climate change. *Proceedings of the National Academy of Sciences of the United States of America* 113.22: 6230–6235.**

Based on 4,556 global fish surveys, the authors analyze how twenty-five different environmental drivers as well as fish biodiversity affect fish biomass. Key predictors of fish biomass increase were fish species richness, functional diversity, and mean temperature. Temperature increases fish biomass directly, as well as indirectly by increasing fish diversity. In contrast, temperature variability had a negative effect on fish biomass, but this effect was halved in the richest fish communities. Hence, the authors conclude that biodiversity can buffer fish biomass against the effects of climate change.

**Nyboer, E. A., H. Y. Lin, J. R. Bennett, et al. 2021. Global assessment of marine and freshwater recreational fish reveals mismatch in climate change vulnerability and conservation effort. *Global Change Biology* 27.19: 4799–4824.**

Uses physiological and ecological traits of 415 recreational fisheries species from marine and freshwater habitats to assess their vulnerability to climate change. Finds that >20% of the studied species showed climate change vulnerability, in particular for coral reef fishes and freshwater fishes. Further uses socioeconomic values and conservation efforts to detect potential mismatches between species at risk and conservation efforts, with the analysis covering spatial as well as taxonomic scales.

**Pörtner, H. O., and M. A. Peck. 2010. Climate change effects on fishes and fisheries: Towards a cause-and-effect understanding. *Journal of Fish Biology* 77.8: 1745–1779.**

Evaluates the potential impacts of changes in CO<sub>2</sub>, dissolved O<sub>2</sub>, and temperature, as a result of climate change, on the physiology of fishes, and the potential consequences at the population and ecosystem levels. Includes quantitative analyses of the upper and lower thermal tolerances of fishes from different latitudes (and hence environmental temperature). Uses studies from around the world to reveal a relationship between acclimation temperature and thermal tolerance. The effects of ontogeny on thermal tolerances are also evaluated.

**Sampaio, E., C. Santos, I. C. Rosa, et al. 2021. Impacts of hypoxic events surpass those of future ocean warming and acidification. *Nature Ecology & Evolution* 5.3: 311–321.**

Meta-analysis for fishes, mollusks, and crustaceans on the effects of ocean warming, acidification, and hypoxia on various traits, including survival, growth, and metabolism. For fishes, the effects of hypoxia on these three traits were consistently negative, across tropical and temperate species as well as life stages. In contrast, the effects of ocean warming and acidification were smaller than for hypoxia or non-significant. The important effects of hypoxia call for multi-stressor designs that include reduced O<sub>2</sub> concentrations.

**Vergés, A., P. D. Steinberg, M. E. Hay, et al. 2014. The tropicalization of temperate marine ecosystems: Climate-mediated changes in herbivory and community phase shifts. *Proceedings of the Royal Society B: Biological Sciences* 281.1789: 20140846.**

Reviews the extent of range extensions by tropical herbivorous fishes into temperate ecosystems and how they alter these systems through overgrazing of canopy-forming algae and seagrasses, which can lead to habitat phase shifts. Several mechanisms are proposed, relating to functional differences in grazing by tropical versus temperate herbivores, and differences in traits and nutritional value of tropical versus temperate macrophytes.

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## Ecophysiology

Many of the threats to the persistence of fish populations under climate change have physiological underpinnings best understood via the inherently integrative discipline of physiological ecology. Under this discipline, biophysical and biochemical mechanisms used by individual organisms to cope with changing environmental conditions can help build a framework to understand ecological interactions at population and ecosystem levels, as Tracy, et al. 1983 describes. When a fish perceives a stressor and initiates a primary, secondary, or tertiary stress response, the measurements that physiological ecologists may make can be used as biomarkers to help interpret how homeostasis is either disrupted/reestablished, or maintained under new conditions, as per Barton 2002. Primary stress responses usually occur at the hypothalamic-pituitary-adrenal (HPA) axis, releasing catecholamines and corticosteroids (glucocorticoids) into circulation, as described in Wendelaar Bonga 1997. Secondary stress responses (e.g., heat shock proteins [HSPs], hematological parameters, etc.) can activate metabolic, cardiorespiratory, immune, and ion-balance pathways, as Mommsen, et al. 1999 outlines. Tertiary stress responses may include behaviors influencing movement, growth, and disease, as Wedemeyer, et al. 1990 suggests. With clear connections to biological fitness, the stress response can have immediate (e.g., fight or flight) and long-term adaptive advantages but can be maladaptive if growth, feeding, digestion, immune function, and/or reproduction are implicated, as Barton and Iwama 1991 and Chrousos 1998 describe. Indeed, via physiological ecology, stress biomarkers can be monitored between species, activities, life history stages, environmental conditions, and over spatial and temporal scales. For example, upon progressive exposure to marine heat-wave conditions over five weeks, Johansen, et al. 2021 identifies various biomarker responses in two coral reef fish species, *Caesio cuning* and *Cheilodipterus quinquelineatus*. Rapid responses to the simulated heatwave occurred in muscle metabolic enzyme activities, hematological parameters, and respiratory morphology in the active, mobile *C. cuning*, but later and to a lesser extent in the more sessile, territorial *C. quinquelineatus*. Such cardiorespiratory and metabolic performance biomarkers, along with antioxidant chaperones (e.g., catalase, ubiquitin, lipid peroxidase), as found in Madeira, et al. 2017, and changes in metabolic, immune, and HSP gene expression patterns, as outlined in Bernal, et al. 2020, may help evaluate the timescale over which fish species acutely respond to heatwaves or acclimatize to warming over the longer term. While the hormonal underpinnings of the stress responses are well understood, considerable variation still exists across taxa, life history stages, and environmental conditions, emphasizing research priority in this area, especially given that the fishes must respond to not just one but multiple simultaneous stressors occurring with climate change.

**Barton, B. A. 2002. Stress in fishes: A diversity of responses with particular reference to changes in circulating corticosteroids. *Integrative and Comparative Biology* 42.3: 517–525.**

Outlines the primary, secondary, and tertiary stress responses and their implications, especially in the fishes, where the magnitude, duration, and recovery of the glucocorticoid response (i.e., cortisol) and other physiological changes caused by stress are thoroughly discussed. Intraspecific variation and genetic history of an organism in terms of the stress response are also discussed in terms of biological monitoring programs.

**Barton, B. A., and G. K. Iwama. 1991. Physiological changes in fish from stress in aquaculture with emphasis on the response and effects of corticosteroids. *Annual Review of Fish Diseases* 1:13–26.**

Unravels the adaptive and maladaptive significance of a stress response, particularly in the fishes, and how disrupting and reestablishing or maintaining homeostasis can implicate a fish's health. Focuses on the mechanistic basis for the stress response in terms of the hypothalamic-pituitary-interrenal axis and the resultant elevation of circulating corticosteroids and consequences in terms of immune function, reproduction, growth, and metabolism.

**Bernal, M. A., C. Schunter, R. Lehmann, et al. 2020. Species-specific molecular responses of wild coral reef fishes during a marine heatwave. *Science Advances* 6.12: eaay3423.**

Uses liver transcriptomes to understand the molecular response of five coral reef fish species to the 2016 marine heatwave that plagued the Great Barrier Reef, Australia. Finds that gene expression patterns that related to certain physiological mechanisms were species-specific and influenced by the duration of elevated temperature exposure. Emphasizes the importance of considering the effects of extreme warming events when evaluating the consequences of climate change on fish communities.

**Chrousos, G. P. 1998. Stressors, stress, and neuroendocrine integration of the adaptive response. *Annals of the New York Academy of Sciences* 851.1: 311–335.**

Thorough overview of the behavioral and physical responses to acute stress. Organizes the information around the major endocrine axes, behavior, and both gastrointestinal and immune responses. Moreover, it discusses long-term effects of acute stress on growth and development that could also have chronic endocrine, metabolic, cardiovascular, psychiatric, or immunological implications.

**Johansen, J. L., L. E. Nadler, A. Habary, A. J. Bowden, and J. L. Rummer. 2021. Thermal acclimation of tropical reef fishes to global heatwaves. *eLife* 10:e59162.**

Investigates how acute heating events—days to months—can elicit acclimation responses in coral reef fishes. Documents eighteen metabolic and cardiorespiratory changes occurring in the gills, blood, spleen, and muscles in two coral reef fish species over five weeks of thermal stress. The onset and duration of biomarker responses differed between species, but seven biomarkers proved critical in evaluating acclimation progression and completion and could help evaluate thermal responses across other coral reef fish species as well.

**Madeira, C., D. Madeira, M. S. Diniz, H. N. Cabral, and C. Vinagre. 2017. Comparing biomarker responses during thermal acclimation: A lethal vs non-lethal approach in a tropical reef clownfish. *Comparative Biochemistry and Physiology A: Molecular & Integrative Physiology* 204:104–112.**

Measures thermal stress biomarkers (heat shock protein [Hsp70] and total ubiquitin) in clownfish (*Amphiprion ocellaris*) while simulating heat-wave conditions. Muscle and fin were sampled under control and elevated temperature treatments to compare lethal to nonlethal sampling methods. Heat shock responses were highly inducible within a week in muscle but not in fin tissue, indicating that the latter is not reliable for monitoring. No mortality was documented under either treatment, however, suggesting that *A. ocellaris* may exhibit acclimation potential under ocean warming.

**Mommsen, T. P., M. M. Vijayan, and T. W. Moon. 1999. Cortisol in teleosts: Dynamics, mechanisms of action, and metabolic regulation. *Reviews in Fish Biology and Fisheries* 9:211–268.**

Summarizes the role of cortisol as the principal corticosteroid in teleost fishes and how concentrations in the plasma rise dramatically during stress. Notes the relationship between plasma cortisol and various metabolic consequences and the debates that have been brought forth in the literature that have been largely centered around species-specific responses, methodologies, sampling techniques, and exposure duration. Nonetheless, it conveys common themes on the physiological and metabolic roles of cortisol in teleost fishes.

**Tracy, C. R., J. S. Turner, G. A. Bartholomew, et al. 1983. What is physiological ecology? *Bulletin of the Ecological Society of America* 63.4: 340–347.**

Commentary that discusses the definition of the hybrid discipline of physiological ecology, especially in terms of its parent disciplines, and its importance in understanding how ecosystems operate in a changing biosphere and in explaining migrations and geographical distributions of taxa. Highlights that while biology is a continuum, to study it requires it to be subdivided logically. Moreover, while data that are collected are primarily physiological, they must be interpreted through an ecology lens.

**Wedemeyer, G. A., B. A. Barton, and D. J. McLeay. 1990. Stress and acclimation. In *Methods for fish biology*. Edited by C. B. Schreck and P. B. Moyle, 451–489. Bethesda, MD: American Fisheries Society.**

Provides an overview as to how physiological systems of fishes can be severely challenged or “stressed” by a variety of biological, chemical, and physical factors. The importance of understanding tolerance limits for various stress factors and the potential for acclimation is emphasized, especially in the context of species-habitat relationships, disease prevention, conservation, and resource management. Definitions and terms are communicated, and the importance of their proper use are underscored.

**Wendelaar Bonga, S. E. 1997. The stress response in fish. *Physiological Reviews* 77.3: 591–625.**

Documents the similarities between the stress response in teleost fishes to that of terrestrial vertebrates, especially in terms of the principal messengers of the brain-sympathetic-chromaffin (or adrenal medulla) and brain-pituitary-interrenal (or adrenal) axes as well as their functions, involving oxygen uptake and transport, energy mobilization, reallocation of energy away from growth and reproduction, and suppressive effects on immune functions. Major differences between teleosts and terrestrial vertebrates are related to the aquatic environment and resulting hydromineral disturbances and toxicant exposure.

## Behavior

In animal conflicts, the success of one species' chosen strategy depends on the strategies of coexisting species. Whalen, et al. 2020 suggests that competition over resources, such as habitat and food, drives variation in traits across geographic regions. Goldenberg, et al. 2018 shows that as climate stressors affect the quality of resources, these contests will become more frequent. Game theory is increasingly used to predict the outcome of competitive interactions that arise during the acquisition of resources and has been applied to analyze the evolution of phenotypes as the environment changes. Hugie and Dill 1994 suggests that such contests can be predicted by differences in habitat and behavior, with game theory predicting that these differences will settle disputes and whether a behavioral strategy is evolutionarily stable. However, the stability of such behaviors depends on species-specific tolerances to environmental change. For example, Hu, et al. 2022 finds that the effects of climate change are complex owing to the different physiological tolerances of individual species, but also the tolerances of interacting species, which can affect the way animals distribute themselves as well as their foraging behavior when resources are limited. This can have the net effect of disrupting evolutionarily stable behaviors, including those that have evolved to infer obvious fitness enhancing benefits such as shoaling. Mitchell, et al. 2022 demonstrates that exposure to ocean acidification and warming reduced shoal performance, leading to decreased shoal cohesion and lateralization. Domenici, et al. 2017 reviews the effects of hypoxia on schooling and finds similar disruptions to school formation. Taken together, these studies suggest the benefits of group living may be altered under projected future ocean conditions. The mechanisms underpinning these changes are likely due to interference in the processing of sensory information. Domenici, et al. 2019 notes that exposure to climate change stressors can disrupt the way in which important sensory cues are perceived. Draper and Weissburg 2019 provides a systematic review on the effects of warming and acidification on predator-prey interactions through the lens of sensory ecology. Heuer and Grosell 2014 suggests that impaired behavior function following exposure to ocean acidification is likely due to disruption of multiple physiological systems, including neurosensory systems. In a landmark study, Nilsson, et al. 2012 demonstrates that exposure to elevated CO<sub>2</sub> disrupted acid-base levels in the neuronal cleft, and in doing so altered normal neuronal cell membrane ion gradients, affecting the firing of an important class of neuroreceptors, known as GABA-A receptors. This was further supported when fish that were treated with gabazine, a GABA<sub>A</sub> receptor antagonist, were found to have restored sensory behaviors. However, Clark, et al. 2020 shows contrasting behavioral responses of fish under elevated CO<sub>2</sub> levels, which has resulted in a large debate over experimental reproducibility in fish behavioral studies related to ocean acidification.

**Clark, T., G. Raby, D. Roche, et al. 2020. Ocean acidification does not impair the behaviour of coral reef fishes. *Nature* 577:370–375.**

Tested the effects of elevated CO<sub>2</sub> on the sensory and behavioral responses of several tropical damselfish species. Did not find an attraction by damselfishes to predator chemical cues due to the effects of ocean acidification, in contrast to some previous studies.

Found no negligible effects of ocean acidification on damselfish activity levels and lateralization, in contrast to some previous studies.

**Domenici, P., B. J. Allan, C. Lefrançois, and M. I. McCormick. 2019. The effect of climate change on the escape kinematics and performance of fishes: Implications for future predator-prey interactions. *Conservation Physiology* 7.1: coz078.**

Reviews the effect of ocean acidification, warming, and hypoxia on the locomotory and sensory behaviors that underpin escape performance in fish. Found that warming had the most consistent and negative effect on escape performance when compared to hypoxia and acidification, and that the magnitude of effects would depend on individual sensitivities.

**Domenici, P., J. F. Steffensen, and S. Marras. 2017. The effect of hypoxia on fish schooling. *Philosophical Transactions of the Royal Society B: Biological Sciences* 372.1727: 20160236.**

Reviews the effects of hypoxia on school structure and dynamics and concludes that hypoxia disrupts school formation and cohesion, and that large schools can exacerbate hypoxic conditions by reducing oxygen through the axis of motion as a consequence of the oxygen consumed by the individuals swimming at the front of the school.

**Draper, A. M., and M. J. Weissburg. 2019. Impacts of global warming and elevated CO<sub>2</sub> on sensory behavior in predator-prey interactions: A review and synthesis. *Frontiers in Ecology and Evolution* 7:72.**

Systematic review on the effects of warming and acidification on predator-prey interactions based on sensory ecology. Evaluates alterations to sensory cue production, transmission, and reception, and how this may affect predator-prey interactions. Also discusses the importance of multimodal cues and sensing.

**Goldenberg, S. U., I. Nagelkerken, E. Marangon, A. Bonnet, C. M. Ferreira, and S. D. Connell. 2018. Ecological complexity buffers the impacts of future climate on marine consumers. *Nature Climate Change* 8.3: 229–233.**

By using the combination of a large mesocosm experiment with a global meta-analysis, the authors demonstrate that fish may be able to mitigate the impacts of elevated CO<sub>2</sub>, through changes in resource abundance. However, this was coupled with increased risk-taking under ocean warming, which may increase the vulnerability of consumers to predation.

**Heuer, R. M., and M. Grosell. 2014. Physiological impacts of elevated carbon dioxide and ocean acidification on fish. *American Journal of Physiology: Regulatory, Integrative and Comparative Physiology* 307.9: R1061–R1084.**

Extensive review on the physiological mechanisms that may underpin observed changes in neurosensory and behavioral endpoints, otolith growth, mitochondrial function, and metabolic rate. Authors suggest that impairment is likely due to increases in pCO<sub>2</sub> and HCO<sub>3</sub> that occur in the body during pH compensation for acid-base balance, and conclude that ocean acidification causes significant effects on fish across multiple physiological systems.

**Hu, N., P. E. Bourdeau, C. Harlos, Y. Liu, and J. Hollander. 2022. Meta-analysis reveals variance in tolerance to climate change across marine trophic levels. *Science of the Total Environment* 827:154244.**

Extensive meta-analysis using 1,278 experiments spanning 236 species and 18 phyla to determine trophic differences in response to climate change in ectothermic animals, including freshwater, marine, and terrestrial. Found that herbivores were the most sensitive to climate change and that higher trophic levels higher display greater tolerance.

**Hugie, D. M., and L. M. Dill. 1994. Fish and game: A game theoretic approach to habitat selection by predators and prey. *Journal of Fish Biology* 45 (Supplement A): 151–169.**

Applies a game-theoretic approach to study a generalized habitat selection game between predators and prey. Overall findings suggest that prey prefer habitat where predator search rates or capture efficiency is compromised and that habitat choice decisions of prey are not driven by differences in habitat productivity.

**Mitchell, A., D. J. Booth, and I. Nagelkerken. 2022. Ocean warming and acidification degrade shoaling performance and lateralization of novel tropical-temperate fish shoals. *Global Change Biology* 28.4: 1388–1401.**

Tests the effect of ocean warming and acidification on shoaling dynamics (lateralization and boldness) in two shoal types (mixed species and temperate). Demonstrates that lateralization and school cohesion decrease under future ocean scenarios. Tropical fish become bolder under acidification, while acidification dampened boldness in temperate fish. Concludes that group behaviors may be altered under projected future ocean conditions.

**Nilsson, G. E., D. L. Dixson, P. Domenici, et al. 2012. Near-future carbon dioxide levels alter fish behavior by interfering with neurotransmitter function. *Nature Climate Change* 2.3: 201–204.**

Demonstrates that abnormal behaviors exhibited by some coral reef fish exposed to high CO<sub>2</sub> were due to impairment of GABA-A receptors and that behaviors could be restored by treatment with an antagonist of the GABA-A receptor.

**Whalen, M. A., R. D. Whippo, J. J. Stachowicz, et al. 2020. Climate drives the geography of marine consumption by changing predator communities. *Proceedings of the National Academy of Sciences of the United States of America* 117.45: 28160–28166.**

Large field experiment measuring the feeding intensity of generalist marine consumers across forty-two sites around the globe. Demonstrates that feeding intensity away from the equator is better explained by the presence of particular consumer families than by latitude or temperature, and conclude that changes in biodiversity can have equal to or larger impacts on ecological processes than climate change.

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## Life Histories and Ecological Niches

Life histories and niche differentiation provide categorization approaches allowing general expectations on the responses of species to climate change. For example, species that exhibit resource specialization, such as food and habitat, are expected to be at greater risk with climate change when their necessary resources are reduced, as has been seen for coral reef or kelp-reliant fishes in Stuart-Smith, et al. 2021. However, life history and ecological niches are not static between populations and individuals. Wang, et al. 2020 reveals life-history traits, including faster growth, earlier maturation, and higher mortality occurred in populations found at warmer temperatures. Sánchez-Hernández, et al. 2021 observes that freshwater generalist consumers have the capacity to be flexible in diet depending on water temperature and prey availability in lakes. Furthermore, ecological niches are important for range shifting species, with omnivory and latitudinal range size increasing range extension rate, as shown in Sunday, et al. 2015. Consistently for fishes, particular life stages appear to be more sensitive to climate change, especially temperature, and represent potential bottlenecks to future persistence. Physiological tolerance patterns place spawners and embryos at the great risk for abnormal ocean temperatures as shown in the meta-analysis Dahlke, et al. 2020. Reproduction in both freshwater and marine species generally only occurs within a restricted seasonal window, which means it also has evolved to occur within a narrow thermal window. Taylor 2007 shows that environmental warming has already resulted in shifts in the timing of migration events for reproduction in pink salmon, while Crozier, et al. 2020 utilizes a heat-wave event to model 80 percent likely reduction in future survival or a need to shifting migration timing by two weeks for the population of adult sockeye salmon. High thermal sensitivity of reproduction has also been observed in tropical fish, with small increase in temperature resulting in reductions in fecundity and quality of progeny. Interestingly, the combined work of Miller, et al. 2013 and Miller, et al. 2015 shows that the impacts of warming on reproduction were far greater than ocean acidification, which instead stimulated enhanced reproduction.

**Crozier, L. G., J. E. Siegel, L. E. Wiesebron, et al. 2020. Snake River sockeye and Chinook salmon in a changing climate: Implications for upstream migration survival during recent extreme and future climates. *PLoS One* 15:e0238886.**

Uses a historical database of 17,279 migrating fish that included the Pacific marine heat-wave event in 2015 to model the effect of future climate change (expected in 2040s) to migration timing and survival of Chinook and sockeye salmon. For Chinook salmon, adult survival dropped by 4–15 percent, while for sockeye, survival dropped by ~80 percent unless migration shifted to more than two weeks earlier.

**Dahlke, F. T., S. Wohlrab, M. Butzin, and H. O. Pörtner. 2020. Thermal bottlenecks in the life cycle define climate vulnerability of fish. *Science* 369:65–70.**

Meta-analysis comparing the thermal tolerance limits (thermal maximum—thermal minimum) of 694 marine and freshwater fish, finding that thermal limits depend on life stage. Spawners and embryos are the most vulnerable life stages to warming, and reproduction is likely to be the critical bottleneck with future climate change.

**Miller, G. M., F. J. Kroon, S. Metcalfe, and P. L. Munday. 2015. Temperature is the evil twin: Effects of increased temperature and ocean acidification on reproduction in a reef fish. *Ecological Applications* 25:603–620.**

Temperature increases projected by mid- and end-of-the-century (+1.5 and +3°C) caused substantial reductions in reproduction of the cinnamon anemonefish, while elevated CO<sub>2</sub> (644 and 1134 µatm) in combination with ocean warming had little effect on reproduction. Effects of warming on reproduction were linked to negative effects on reproductive hormones, rather than trade-offs due to increased metabolic costs of increased temperature.

**Miller, G. M., S-A. Watson, M. I. McCormick, and P. L. Munday. 2013. Increased CO<sub>2</sub> stimulates reproduction in a coral reef fish. *Global Change Biology* 19:3037–3045.**

Finds stimulation of reproductive output in the cinnamon anemonefish when exposed to moderate (584 µatm) and high (1032 µatm) levels of near future CO<sub>2</sub> for nine months. Over twice as many pairs reproduced in the moderate and high CO<sub>2</sub> conditions. Pairs in high conditions produced twice as many clutches with more eggs per clutch, resulting in 82 percent higher reproductive output.

**Sánchez-Hernández, J., B. Hayden, C. Harrod, and K. K. Kahilainen. 2021. Population niche breadth and individual trophic specialisation of fish along a climate-productivity gradient. *Reviews in Fish Biology and Fisheries* 31:1025–1043.**

Uses a space-for-time approach incorporating environmental gradients, lake morphometry, fish communities, prey availability, and feeding for fifteen fish taxa from various thermal guilds from thirty-five subarctic lakes. Patterns from generalist fish species, one cold-water adapted and one cool-water adapted, similarly switched from consumption of zooplankton in cooler, less productive lakes, to macrozoobenthos in warmer, more productive lakes.

**Stuart-Smith, R. D., C. Mellin, A. E. Bates, and G. J. Edgar. 2021. Habitat loss and range shifts contribute to ecological generalization among reef fishes. *Nature Ecology and Evolution* 5:656–662.**

Calculates a species generalization index that empirically represents the habitat niche breadth for 1,342 reef fish species, showing that the proportion of ecological specialists decreases as a result of climate-driven habitat loss. Demonstrates that generalist tropical reef fishes were better able to colonize subtropical and temperate areas than specialists, suggesting that generalists will be less impacted by growing anthropogenic pressures.

**Sunday, J. M., G. T. Pecl, S. Frusher, et al. 2015. Species traits and climate velocity explain geographic range shifts in an ocean-warming hotspot. *Ecology Letters* 18:9: 944–953.**

Explores how species traits and climate velocity were linked to range extensions in the ocean-warming hot spot of southeast Australia. Including species traits in addition to climate change velocity more than doubled the variation explained, with increased dispersal capacity and ecological generalism promoting range extensions. Specifically, species with greater swimming ability, omnivory, and latitudinal range size all had positive relationships with range extension rate.

**Taylor, S. G. 2007. Climate warming causes phenological shift in pink salmon, *Oncorhynchus gorbuscha*, behavior at Auke Creek, Alaska. *Global Change Biology* 14:229–235.**

A thirty-four-year data set was used to investigate environmental trends at Auke Lake and how they link to pink salmon migration. For the period 1972–2005, average water temperatures for this lake warmed by 0.03°C per year and migration of fry shifted by 0.5 day earlier per year.

**Wang, H. Y., S. F. Shen, Y. S. Chen, Y. K. Kiang, and M. Heino. 2020. Life histories determine divergent population trends for fishes under climate warming. *Nature Communications* 11:4088.**

Investigates patterns of population-level life history traits with sea-surface temperature for 332 Indo-Pacific marine fishes. Found that reef and demersal fishes were more sensitive to water temperature than pelagic and bathydemersal species. There were generally positive effects of temperature on growth, reproduction and natural mortality.

## Consumer-Resource Interactions and Food Webs

Climate change has important consequences for how aquatic taxa interact within the context of their food web and environment. Nagelkerken and Connell 2015 shows that climate change may lead to shifts in consumer behavior, in addition to influencing interactions with other equally important variables such as prey availability and foraging efficiency. Werner and Hall 1974 suggests that foraging efficiency is best described by optimal foraging models, which predict that animals select prey with the lowest cost, thus maximizing their fitness under some environmental constraint (e.g., predation risk). When a predator attacks, prey are faced with a series of decisions, such as how fast to respond, which direction to turn, and how far to escape. Allan, et al. 2013 shows that these decisions can be reduced to a series of different components, each relating to sensory and locomotory capacity, and that the behavioral decisions that underpin escape performance have to occur within milliseconds, and if delayed can lead to increased mortality. In a comprehensive review, Domenici, et al. 2019, cited under Behavior, finds that exposure to climate change stressors alters the processing of sensory information, directly influencing the behavioral basis that governs the outcome of a predator-prey interaction. Grigaltchik, et al. 2012 concludes that the dynamics of predator-prey interactions under future ocean conditions will depend on the extent to which the interacting species are affected and can adapt to the adverse effects of climate change. Yet experiments that enhance ecological complexity by including multiple species, habitats, and trophic levels show that despite the wide-observed impacts of ocean acidification on predator-prey relationships in laboratory experiments, under natural conditions elevated CO<sub>2</sub> can enhance survival of higher trophic levels due to increased primary productivity, as shown in Sswat, et al. 2018. Despite the increased productivity under ocean acidification, Nagelkerken, et al. 2020 shows that when ocean warming and acidification are combined, the food web will contract at the center, and is eventually likely to collapse.

**Allan, B. J., P. Domenici, M. I. McCormick, S. A. Watson, and P. L. Munday. 2013. Elevated CO<sub>2</sub> affects predator-prey interactions through altered performance. *PLoS One* 8.3:e58520.**

Tests the effect of ocean acidification on staged predator-prey interactions in coral reef fish. When predators were exposed to elevated CO<sub>2</sub>, they had reduced capture success when paired with prey exposed to present-day CO<sub>2</sub>. Concludes that the dynamics of predator-prey interactions under future CO<sub>2</sub> environments will depend on the extent to which the interacting species are affected.

**Grigaltchik, V. S., A. J. Ward, and F. Seebacher. 2012. Thermal acclimation of interactions: differential responses to temperature change alter predator-prey relationship. *Proceedings of the Royal Society B: Biological Sciences* 279.1744: 4058–4064.**

Using two freshwater fish—Australian bass (*Macquaria novemaculeata*, predator) and the mosquitofish (*Gambusia holbrooki*, prey)—the authors tested whether interspecific differences in thermal acclimation capacity would modulate predator-prey interactions. Overall, it was found that thermal acclimation affected interactions between species. The authors suggest that inter/intraspecific thermal sensitivity may be a mechanism by which global warming affects ecological communities.

**Nagelkerken, I., and S. D. Connell. 2015. Global alteration of ocean ecosystem functioning due to increasing human CO<sub>2</sub> emissions. *Proceedings of the National Academy of Sciences of the United States of America* 112.43: 13272–13277.**

Extensive meta-analysis of 632 published experiments that quantified the effects of ocean acidification and warming on a suite of ecological end points, including species diversity, species community abundances, and species performance. Overall, it was found that warming and acidification may lead to biotic homogenization with reduced energy flow among trophic levels with little scope for acclimation.

**Nagelkerken, I., S. U. Goldenberg, C. M. Ferreira, H. Ullah, and S. D. Connell. 2020. Trophic pyramids reorganize when food web architecture fails to adjust to ocean change. *Science* 369.6505: 829–832.**

Authors used large mesocosms containing a wide range of species and habitats, and unfiltered inflowing water to allow propagules to naturally enter the tanks. After several months of exposure to elevated CO<sub>2</sub> and warming, they found that ocean acidification in isolation boosted the entire food web from the bottom up in terms of productivity as well as standing biomass. Combined with warming however, the food web was truncated in the center with less energy flow to the top, and the authors speculated that this would ultimately cause the food webs to collapse into shortened bottom-heavy food webs.

**Sswat, M., M. H. Stiasny, J. Taucher, et al. 2018. Food web changes under ocean acidification promote herring larvae survival. *Nature Ecology & Evolution* 2.5: 836–840.**

Used large mesocosms floating in the ocean exposed to ambient and elevated CO<sub>2</sub> conditions for about 3.5 months. The authors observed that ocean acidification increased primary production and hence also prey abundance (zooplankton) for the Atlantic herring. As a result, this carnivorous fish species experienced enhanced survival rates. The authors concluded that the direct negative effects of ocean acidification on larval survival are smaller than the indirect positive effects on larval survival through enhanced food abundance.

**Werner, E. E., and D. J. Hall. 1974. Optimal foraging and the size selection of prey by the bluegill sunfish (*Lepomis macrochirus*). *Ecology* 55.5: 1042–1052.**

Authors constructed a model relating search and handling time to energy return to determine the optimal breadth of diet for the bluegill sunfish. It demonstrates that at low abundances, prey of different size are eaten as encountered. As prey abundance increases, size classes are dropped sequentially from the diet. Authors conclude that these changes in diet maximize return with respect to time spent foraging.

## Competition and Density Dependence

Key climate stressors in the aquatic environment affect biotic interactions among fishes. Environmental warming under climate change will change biotic interactions among species, which will affect predictions of warming impacts, as shown in Huey, et al. 2012. Intra- and interspecific competition, for example, may be strengthened/weakened or made more or less asymmetrical as sea temperatures rise. McCormick, et al. 2013 found that under elevated CO<sub>2</sub> levels, two species of coral-reef damselfish are expected to swap their competitive dominance. Milazzo, et al. 2013 reports that the combined effects of warming and increased relative dominance of a warm-water species cause relocation to a less-preferred habitat of a cool-water species. Booth, et al. 2014 demonstrated that a suite of co-occurring estuarine fishes each had a different growth/temperature relationship such that ambient warming of only a few degrees centigrade would have switched ranked growth rates. Density dependence of key fitness characteristics of fishes may alter under climate change–driven water temperature rises. Watson, et al. 2022 showed for New Zealand stream fishes in the genus *Galaxias* that water temperature interacted with fish density to affect growth rates. Less predictably, Booth 2020 observed that severe storms (e.g., East Coast lows in Australia), which are predicted to strengthen under climate change, initially directly extirpated, but later indirectly facilitated arrival of vagrant coral reef fish into temperate waters, by removing macroalgae and exposing preferred urchin barrens habitat. Rolls, et al. 2017 discussed how climate change can alter three distinct aspects of species invasions: (1) the vulnerability of ecosystems to be invaded, (2) the potential for species to spread and invade new habitats, and (3) the subsequent ecological effects of invaders. Inter-specific competition can ameliorate or exacerbate climate change impacts, as shown in Helland, et al. 2011, while Myrvold and Kennedy 2017 showed that growth can become more density-dependent under climate change.

**Booth, D. J. 2020. Opposing climate-change impacts on poleward-shifting coral-reef fishes. *Coral Reefs* 39:577–581.**

Shows how climate-related storm activity can affect establishment of range-shifting tropical fish species. The storm reduced population sizes of tropical vagrants in temperate waters, but also considerably increased barren habitat, which subsequently facilitated high tropical fish recruitment the following year.

**Booth, D. J., D. E. Poulos, J. Poole, and D. A. Feary. 2014. Growth and temperature relationships for juvenile fish species in seagrass beds: Implications of climate change. *Journal of Fish Biology* 84.1: 231–236.**

Estuarine fish performance (growth) was tested across three water temperatures in Sydney. Southern-distributed species performed best at lower temperatures and northern-distributed fishes at highest temperatures. Predictions were made regarding changes in species dominance as estuary temperatures rise under climate change.

**Helland, I. P., A. G. Finstad, T. Forseth, T. Hesthagen, and O. Ugedal. 2011. Ice-cover effects on competitive interactions between two fish species. *Journal of Animal Ecology* 80:539–547.**

Ice cover, reducing under climate change, affected competition between brown trout and Arctic char. Arctic char grew in darkness and had higher food intake in tank experiments than brown trout. Arctic char exhibited lower energy loss under simulated ice-cover in a semi-natural environment with natural food supply in laboratory experiments. In the field over twenty-five years, brown trout population growth rate depended on the interaction between ice breakup date and Arctic char abundance.

**Huey, R. B., M. R. Kearney, A. Krockenberger, J. A. M. Holtum, M. Jess, and S. E. Williams. 2012. Predicting organismal vulnerability to climate warming: roles of behaviour, physiology and adaptation. *Philosophical Transactions of the Royal Society B: Biological Sciences* 367:1665–1679.**

The vulnerability of a species to environmental change depends on the species' exposure and sensitivity to environmental change, its resilience to perturbations, and its potential to adapt to change. Behavior and physiology are key mechanisms and can affect how well organisms adapt to climate changes in their environments, and models were developed that demonstrate how behavioral thermoregulation can influence vulnerability over time.

**McCormick, M. I., S.-A. Watson, and P. L. Munday. 2013. Ocean acidification reverses competition for space as habitats degrade. *Scientific Reports* 3:3280.**

Experiments showed that for small coral reef fishes, ocean acidification changed competitive outcomes. For two species of damselfishes, the competitively dominant species at current sea conditions was most affected by near-future CO<sub>2</sub> levels, such that they became subordinate at higher CO<sub>2</sub> levels.

**Milazzo, M., S. Mirto, P. Domenici, and M. Gristina. 2013. Climate change exacerbates interspecific interactions in sympatric coastal fishes. *Journal of Animal Ecology* 82:468–477.**

Authors performed a mesocosm experiment and *in situ* observations on the interactive effects of warming and species range extensions of two closely related fish species. They show that the cold-affiliated fish was displaced to less preferred seagrass habitat (as opposed to algal habitat) under elevated temperature and abundance of a warm-affiliated species with whom it interacts in nature increased.

**Myrvold, K. M., and B. P. Kennedy. 2017. Increasing water temperatures exacerbate the potential for density dependence in juvenile steelhead. *Canadian Journal of Fisheries and Aquatic Sciences* 75.6: 897–907.**

Demonstrated that climate-related water temperature changes can exacerbate demographic density dependence in steelhead salmon populations.

**Rolls, R. J., B. Hayden, and K. K. Kahilainen. 2017. Conceptualising the interactive effects of climate change and biological invasions on subarctic freshwater fish. *Ecology and Evolution* 7:4109–4128.**

Climate change, especially through alterations in water temperature, can affect speed and success of invasive species in cold water habitats.

**Watson, A. S., M. J. H. Hickford, and D. R. Schiel. 2022. Interacting effects of density and temperature on fish growth rates in freshwater protected populations. *Philosophical Transactions of the Royal Society B: Biological Sciences* 389:20211982.**

Density-dependent performance of freshwater fishes (*Galaxiidae*) is altered with water temperature, with implications for climate change. Population density, stream temperature, and individual size interact to affect growth rates. When population densities were high, compensatory responses of far slower growth rates were strongest, indicating density dependence.

## Symbiosis, Parasitism, and Disease

Changes in water quality—warming, acidification, and deoxygenation, as well as pollutants—associated with climate change often co-occur with habitat loss and disruptions to predator-prey dynamics that collectively exacerbate parasitic interactions among the fishes, as shown in Artim, et al. 2020. Yet fish-parasite interactions have not been as well studied, largely due to parasite diversity and crypticity. While symbiotic relationships among fishes naturally occur in the wild—at grooming and cleaning stations, for example, as is well studied in Grutter, et al. 2003—some parasitic interactions can be perceived as stressors. Repercussions can be toward growth, development, reproduction, immune responses, aerobic scope, and swimming performance, including fast starts associated with prey capture or predator evasion, as documented in Allan, et al. 2020, all with acute and/or chronic ramifications, as Welicky, et al. 2018 suggests. Immediate trade-offs may occur at the level of behaviors and movement (e.g., drag) if the fish cannot rid itself of parasites, for example, by using cleaning stations, as studied in Demaire, et al. 2020. Over the longer term, immune-compromised individuals and the associated stress responses can lead to disease, population collapse, and declining ecosystem health, making it imperative that fish-parasite relationships are better understood, especially in light of increasing severity and frequency of climate change stressors.

**Allan, B. J. M., B. Illing, E. P. Fakan, et al. 2020. Parasite infection directly impacts escape response and stress levels in fish. *Journal of Experimental Biology* 223.16: jeb230904.**

Highlights the importance of parasites as micro-predators, while rarely causing direct mortality but rather sublethal effects via the energetic tax they cause their host. The study investigated this via experimental gnathiid infection on the swimming and escape performance of a newly settled coral reef fish. Authors measured decreases in fast-start escape performance and swimming behavior and a doubling of cortisol levels. Their findings suggest altered fitness-related traits and acute stress during early life stages may impact recruitment to adult populations.

**Artim, J. M., M. D. Nicholson, G. C. Hendrick, M. Brandt, T. B. Smith, and P. C. Sikkel. 2020. Abundance of a cryptic generalist parasite reflects degradation of an ecosystem. *Ecosphere* 11:e03268.**

Highlights the importance of considering parasites in terms of the metrics used to communicate ecosystem function. The study investigated their hypothesis—ectoparasites increase in abundance as ecosystem function declines—on Caribbean coral reefs. The team observed a negative correlation between the abundance of small gnathiid parasites and live coral, the ecosystem engineer and a natural predator of gnathiids. The study suggests that hyperabundance of generalist parasites, when used in combination with coral cover, can help communicate ecosystem vulnerability.

**Demaire, C., Z. Triki, S. A. Binning, G. Glauser, D. G. Roche, and R. Bshary. 2020. Reduced access to cleaner fish negatively impacts the physiological state of two resident reef fishes. *Marine Biology* 167:48.**

On coral reefs, mutualistic interactions between fishes involving cleaning stations are thought to benefit both the “client” and the “cleaner,” but the physiological underpinnings are not understood. In this study, researchers removed cleaning services for two species of coral reef fishes and later drew blood to look for trade-offs in terms of growth, aerobic capacity, immune activation, and/or reproduction. Their results suggest that even a short-term reduction in access to cleaning services can have negative physiological outcomes, making these relationships important to coral reef ecosystem health.

**Grutter, A. S., J. M. Murphy, and J. H. Choat. 2003. Cleaner fish drives local fish diversity on coral reefs. *Current Biology* 13.1: 64–67.**

Examines cleaner fish abundance and size on coral reefs and how that affects activity of other fish species. The authors experimentally removed cleaner fish (*Labroides dimidiatus*) from reefs for eighteen months and found fish diversity decreased by half and abundance decreased down to 25 percent of original levels. Affected species were those that move between reefs rather than resident species, thus demonstrating the impact of one species on many.

**Welicky, R. L., D. C. Parkyn, and P. C. Sikkel. 2018. Host-dependent differences in measures of condition associated with *Anilocra* spp. parasitism in two coral reef fishes. *Environmental Biology of Fishes* 101:1223–1234.**

This study determined the energetic effects of parasitic infections (*Anilocra* spp.) on two coral reef fish species. Infected French grunt had greater percent moisture in the muscle tissue but similar body condition, total muscle tissue calories, and gut content volumes compared to uninfected conspecifics. However, infected brown chromis had reduced body condition but similar percent moisture in the muscle tissue and total muscle tissue calories compared to uninfected conspecifics. This study highlights that even fish from the same genus localities can respond differently to parasites.

## Larval Dispersal, Range Extensions, and Climate Refugia

Dispersal via larval advection on ocean currents is the norm for marine fishes. O'Connor, et al. 2007 shows that swimming speed of dispersing fish larvae is affected by sea temperature, which also influences their pelagic larval duration (i.e., the time over which they develop and are ready to settle on new habitat). Hence, climate change is predicted to increase the dispersal kernel, especially poleward dispersal/range shifts, via strengthening poleward boundary currents, which both lead to increased sea surface temperatures and physical advection of larvae on these currents, as shown by Wilson, et al. 2018. Consequently, poleward range extensions are increasing under climate change. Champion, et al. 2021 empirically shows extensive poleward range shifts of large pelagic fishes under climate change. Given that fish range encompasses success of larval, juvenile, and adult phases, recent poleward range shifts have occurred due to human-caused climate change via strengthening poleward currents and more favorable water temperatures at higher latitudes, while range contractions may occur anti-poleward, as reviewed in Booth, et al. 2011. Perry, et al. 2005 reports that two-thirds of North Sea fish species shifted in mean latitude or depth or both as temperatures rose over twenty-five years, suggesting that climate change is having detectable impacts on marine fish distributions and fish species richness. As climate alters, and species ranges shift, conditions at leading and trailing edges of a species distribution may become intolerable. Refugia may allow a foothold as ranges expand poleward, such as the establishment of a subtropical coral beds off Sydney, Australia, which has facilitated early settlement of a number of coral reef fishes found nowhere else in the area, as observed in Booth and Sear 2018.

**Booth, D. J., N. Bond, and P. I. Macreadie. 2011. Detecting range shifts among Australian fishes in response to climate change. *Marine and Freshwater Research* 62.9: 1027–1042.**

A summary of climate change effects on marine, estuarine, and freshwater fishes, including range shifts and mechanisms. Complications in defining range are outlined, and increases in water temperature, reduced freshwater flows, and changes in ocean currents are likely to be the key drivers of climate-induced range shifts in Australian fishes.

**Booth, D. J., and J. Sear. 2018. Coral expansion in Sydney and associated coral-reef fishes. *Coral Reefs* 37:995.**

Subtropical coral beds off temperate Sydney have facilitated the establishment of several coral reef fishes not recorded in the area before and attracted higher densities of other tropical and temperate fishes. The coral beds have expanded rapidly, and so may increasingly enhance poleward range expansions.

**Champion, C., S. Brodie, and M. A. Coleman. 2021. Climate-driven range shifts are rapid yet variable among recreationally important coastal-pelagic fishes. *Frontiers in Marine Science* 8:622299.**

Coastal-pelagic fish species underwent rapid, yet variable, poleward range shifts, which have implications for ecosystem structure and the changing availability of key resources to fisheries.

**O'Connor, M. I., J. F. Bruno, S. D. Gaines, et al. 2007. Temperature control of larval dispersal and the implications for marine ecology, evolution, and conservation. *Proceedings of the National Academy of Science of the United States of America* 104.4: 1266–1271.**

Advection of larval reef fishes dispersing in ocean currents is modeled to include water temperature effects on swimming speed and larval duration. Temperature effects on metabolism speed up development and shorten pelagic larval duration, but also lead to increased swimming speeds and thus daily movement, which affect dispersal distance in opposing ways.

**Perry, A. L., P. J. Low, J. R. Ellis, and J. D. Reynolds. 2005. Climate change and distribution shifts in marine fishes. *Science* 308:1912–1915.**

Large-scale analysis of distributional shifts in North Sea fish species under twenty-five years of seawater warming. Found that nearly two-thirds of the species shifted their distribution to higher latitudes and/or greater depths. Analyzed the traits associated with range shifts, finding that range shifting species have faster life cycles and smaller body sizes.

**Wilson, S. K., M. Depczynski, R. Fisher, et al. 2018. Climatic forcing and larval dispersal capabilities shape the replenishment of fishes and their habitat-forming biota on a tropical coral reef. *Ecology and Evolution* 8.3: 1918–1928.**

Climate-change-linked El Niño Southern Oscillation strongly affected larval dispersal of tropical marine fish, but this is mediated by functional ecology (e.g., larval behavior).

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## Fish Biodiversity and Fisheries Productivity

The impact of climate change on fish diversity (both functional and taxonomic) has the potential to reduce community stability and resilience to climate impacts and other human stressors. McLean, et al. 2019 analyzes a thirty-three-year time series of fish communities in the North Sea, showing that fish functional diversity decreased with climate change, favoring traits that are more adapted to novel environments. Stuart-Smith, et al. 2021, cited under Life Histories and Ecological Niches, shows that reduced functional diversity can in turn impact ecosystem stability through biotic homogenization and the loss of ecological specialists that perform important ecosystem functions. Mellin, et al. 2016 highlights that fish species traits are important predictors of fish responses to climate change, as long-lived species with late maturation and/or large body sizes are disproportionately impacted. Bates, et al. 2013 additionally shows that geographical range size and heat tolerance promote fish invasion success, which contributes to the erosion of ecosystem stability and resilience to climate impacts through extinctions of native species. In contrast to functional diversity, the impact of climate change on fish taxonomic diversity remains unclear and geographically variable. Chaudhary, et al. 2021 shows that climate change has modified the global gradient in fish species diversity, with mid-latitude marine regions experiencing increases in fish species richness that contributed to a more pronounced dip in species richness around the equator. Fish biomass production and nutritional quality of fisheries catches are impacted by climate change through complex mechanisms, including stock redistribution and compositional shifts following changes in ocean biochemistry. Cheung, et al. 2013 shows that such changes caused a reduction of fish body size, impacting global biomass catches in addition to decreasing fish abundances. Furthermore, Pinsky, et al. 2018 shows that as climate change causes species range shifts and increasingly redistributes fish stocks, many species will likely shift across national boundaries in the future and potentially cause geopolitical conflicts over these newly shared resources. Galappaththi, et al. 2022 reviews the climate stressors relevant to fisheries and their impacts, highlighting different types of fisheries adaptive response to climate change. Regarding changes in nutritional quality of fisheries catches, Mellin, et al. 2022 reviews the direct and indirect mechanisms by which ocean warming can alter fish nutrient concentration. Shalders, et al. 2022 shows that ocean warming and acidification can lead to decreases in seafood macro- and micronutrients. Maire, et al. 2021 shows that climate change threatens micronutrient fisheries yields in 40 percent of the world's countries, with micronutrient-dense catches being particularly vulnerable to climate change.

**Bates, A. E., C. M. McKelvie, C. J. B. Sorte, et al. 2013. Geographical range, heat tolerance and invasion success in aquatic species. *Proceedings of the Royal Society B: Biological Sciences* 280.1772: 20131958.**

Tests the hypothesis that geographical range size and heat tolerance promote invasion success, using a global data set of freshwater and marine fishes and invertebrates. Concludes that introduced species tend to have broader geographical ranges and are more heat tolerant than native species.

**Chaudhary, C., A. J. Richardson, D. S. Schoeman, and M. J. Costello. 2021. Global warming is causing a more pronounced dip in marine species richness around the equator. *Proceedings of the National Academy of Sciences of the United States of America* 118.15: e2015094118.**

Assesses the impact of climate change on the global latitudinal gradient in species richness of fish and other marine organisms. Demonstrates that species richness has declined at the equator and increased at mid-latitudes, in addition to a shift toward the northern hemisphere, particularly among pelagic species.

**Cheung, W. W. L., J. L. Sarmiento, J. Dunne, et al. 2013. Shrinking of fishes exacerbates impacts of global ocean changes on marine ecosystems. *Nature Climate Change* 3.3: 254–258.**

Models fish biological responses to multiple climate change stressors through changes in distribution, abundance, and body size for over six hundred marine fish species. Shows that assemblage-averaged maximum fish body weight is expected to decrease by 14–24 percent globally by 2050 under a high emission scenario. Attributes about 50 percent of this shrinkage to changes in distribution and abundance, and the remainder to changes in physiology.

**Galappaththi, E. K., V. B. Susarla, S. J. T. Loutet, S. T. Ichien, A. A. Hyman, and J. D. Ford. 2022. Climate change adaptation in fisheries. *Fish and Fisheries* 23.1: 4–21.**

Reviews 230 case studies of climate change adaptation in fisheries. Identifies multiple stressors of climate change relevant to global fisheries, showing that 63 percent of studies considered climate change as the key driver for change in fisheries system. Highlights three categories of adaptive responses, including coping mechanisms, adaptive strategies, and management responses.

**Maire, E., N. A. J. Graham, M. A. MacNeil, et al. 2021. Micronutrient supply from global marine fisheries under climate change and overfishing. *Current Biology* 31.18: 4132–4138.**

Couples global assessments of micronutrient content and fisheries catch data to determine the vulnerability of nutrient supplies from fisheries to both climate change and exploitation. Shows that catches with greater species richness are more nutrient dense, but also more vulnerable to climate change. Countries with high prevalence of inadequate micronutrient intake were characterized by fisheries that are highly vulnerable to climate change.

**McLean, M., D. Mouillot, M. Lindegren, et al. 2019. Fish communities diverge in species but converge in traits over three decades of warming. *Global Change Biology* 25.11: 3972–3984.**

Assesses the spatiotemporal dynamics of taxonomic and trait structure for fish communities in the North Sea over a thirty-three-year time series. Shows that fish communities taxonomically diverged over time, but functionally converged toward the same traits, specifically smaller, faster-growing species with an affinity for warm temperatures.

**Mellin, C., C. Hicks, D. A. Fordham, et al. 2022. Safeguarding nutrients from coral reefs under climate change. *Nature Ecology & Evolution* 6:1808–1817.**

Reviews the direct (metabolism, trophodynamics) and indirect (habitat, species range shifts) mechanisms by which global warming is expected to alter the nutritional quality of coral reef fisheries. Outlines future research priorities toward sustainable reef fisheries contributing to food and nutrition security under climate change.

**Mellin, C., D. Mouillot, M. Kulbicki, et al. 2016. Humans and seasonal climate variability threaten large-bodied coral reef fish with small ranges. *Nature Communications* 7.1: 10491.**

Models the environmental and anthropogenic drivers of fish occurrence for 241 coral reef fish species across the Indo-Pacific. Shows that large-bodied species with small geographical ranges have been disproportionately affected by human impact and seasonal climate variability. Identifies the most sensitive species and critical thresholds of human and climatic stressors.

**Pinsky, M. L., G. Reygondeau, R. Caddell, J. Palacios-Abrantes, J. Spijkers, and W. L. Cheung William. 2018. Preparing ocean governance for species on the move. *Science* 360.6394: 1189–1191.**

Projects future distribution shifts for 892 commercially important marine fish and invertebrates. Shows that many of the world's exclusive economic zones are likely to receive new stocks, especially under a business-as-usual greenhouse gas emission scenario. Argues that these new transboundary stocks will likely cause geopolitical conflict unless far-sighted governance strategies are adopted with adaptable agreements between countries.

**Shalders, T. C., C. Champion, M. A. Coleman, and K. Benkendorff. 2022. The nutritional and sensory quality of seafood in a changing climate. *Marine Environmental Research* 176:105590.**

Meta-analysis of fifty-three experimental studies investigating the effects of temperature and pH on the nutritional and sensory quality of seafood (including fish). Shows that effects of elevated temperature and reduced pH on nutritional composition of seafood was variable, with >50% of all species showing a change in fatty acid and protein content.

## Phenotypic Plasticity

There is growing consensus that for many species the rate and magnitude of climate change is too much for adaptation alone to maintain performance, as highlighted in Radchuk, et al. 2019. Due to this concern, studies on the capacity for phenotypic plasticity to maintain future performance and survival have proliferated, generally through the simulation of future conditions in laboratory experiments. Seebacher, et al. 2015 is a comprehensive meta-analysis exploring patterns across taxonomic groups and geographic regions, finding that fish (freshwater and marine) have a high capacity for thermal plasticity across latitudes, even though plastic capacity is expected to be linked to the level of environmental variation naturally experienced. Connecting whether phenotypic plasticity observed in experiments would be adaptive in nature is a critical step to understanding the role that plasticity will play in response to climate change. Petit-Marty, et al. 2021 shows that molecular plasticity to ocean acidification occurring at natural CO<sub>2</sub> seeps and the standing genetic variation available could indicate adaptive potential to future climate change. Milazzo, et al. 2016 and Spatafora, et al. 2021 show behavioral plasticity in wild fish living along volcanic CO<sub>2</sub> gradients, underlining the role of behavioral adjustments as potential mechanisms to buffer the impacts of ongoing environmental changes in the long term. Morgan, et al. 2020 shows that directional selection, which is likely to occur with climate change, can reduce the capacity for plasticity in the trait-critical thermal maximum. This pattern is expected in nature when plasticity plays a role in responding to environmental change but then becomes canalized through selection.

**Petit-Marty, N., I. Nagelkerken, S. D. Connell, and C. Schunter. 2021. Natural CO<sub>2</sub> seeps reveal adaptive potential to ocean acidification in fish. *Evolutionary Applications* 14:1794–1806.**

Fish from volcanic CO<sub>2</sub> seeps exhibited an overall increased gene expression in gonad tissue, with up-regulated genes functionally involved in the maintenance of pH homeostasis and increased metabolism. The patterns of DNA polymorphisms were a deviation from neutral evolution expectations, providing evidence for adaptive selection to ocean acidification. Authors believe the targets of the adaptive selection are likely to be regulatory sequences responsible for the increased expression of these genes.

**Milazzo, M., C. Cattano, S. H. Alonso, et al. 2016. Ocean acidification affects fish spawning but not paternity at CO<sub>2</sub> seeps. *Proceedings of the Royal Society B: Biological Sciences* 283.1835: 20161021.**

Authors studied mating behavior and patterns of paternity of a temperate wrasse at a natural volcanic CO<sub>2</sub> vent. While various behaviors, including male courtship and nest defense, were not altered by elevated CO<sub>2</sub>, pair spawning by dominant male fish was reduced at the vents.

**Morgan, R., M. H. Finnøen, H. Jensen, C. Pélabon, and F. Jutfelt. 2020. Low potential for evolutionary rescue from climate change in a tropical fish. *Proceedings of the National Academy of Sciences of the United States of America* 117.52: 33365–33372.**

As has often been observed in other fishes, a hard upper limit for critical thermal maximum exists for zebrafish. Selection for shifted thermal limits was attempted in the lab by selecting for the highest or lowest thermal tolerance over six generations. An increase in upper thermal tolerance through selection was relatively limited compared to down-selected lines, and the influence that plasticity played in shifting upper thermal maximum decreased across generations.

**Radchuk, V., T. Reed, C. Teplitsky, et al. 2019. Adaptive responses of animals to climate change are most likely insufficient. *Nature Communications* 10:3109.**

This meta-analysis uses birds as a model to test whether phenotypic trait changes are adaptive and associated with climate change. Global warming so far has not consistently affected morphological traits but has advanced phenological traits. Finds that for most species, adaptation is not sufficient to maintain performance in persistence with ongoing climate change.

**Seebacher, F., C. R. White, and C. E. Franklin. 2015. Physiological plasticity increases resilience of ectothermic animals to climate change. *Nature Climate Change* 5:61–66.**

Meta-analysis on physiological plasticity in ectothermic animals, including freshwater, marine, and terrestrial. Finds that freshwater and marine animals, as well as animals from more stable environments, have capacity for plasticity to decrease thermal sensitivity. However, terrestrial species and those from higher latitudes were found to have less capacity for acclimation via phenotypic plasticity.

**Spatafora, D., F. Quattrochi, C. Cattano, F. Badalamenti, and M. Milazzo. 2021. Nest guarding behaviour of a temperate wrasse differs between sites off Mediterranean CO<sub>2</sub> seeps. *Science of the Total Environment* 799:149376.**

Studied a range of behaviors of male temperate wrasses during their breeding season at a natural volcanic CO<sub>2</sub> vent. Found that time spent by the males guarding their nests was reduced at the vents.

## Molecular Plasticity and Epigenetics

While phenotypic plasticity is often viewed from the perspective of shifts in trait performance, the molecular mechanisms of plasticity are of growing interest. Veilleux, et al. 2015 and Bernal, et al. 2018 show that coral reef fish can display phenotypic plasticity if reared in high water temperatures, and this is controlled by the activation of specific metabolic pathways in the liver in order to compensate for the impaired metabolic scope. Furthermore, Ryu, et al. 2018 measures genome-wide epigenetic DNA methylation patterns, and shows that the information of the “new” environmental conditions caused by climate change is passed to the next generation by specific methylate or de-methylate loci, which potentially influence their expression in elevated water temperatures, and which could explain their acclimation via phenotypic plasticity of gene expression. This has been shown in several species, including invertebrates such as corals and sea urchins, for example in Putnam, et al. 2016 and Bogan, et al. 2023. Much remains to be learned about the potential of fishes to adapt to a future climate in terms of selection of beneficial traits that allow fish to survive and reproduce, which plays a role in shaping fish assemblages and ecosystems.

**Bernal, M. A., J. M. Donelson, H. D. Veilleux, T. Ryu, P. L. Munday, and T. Ravasi. 2018. Phenotypic and molecular consequences of stepwise temperature increase across generations in a coral reef fish. *Molecular Ecology* 27.22: 4516–4528.**

Measures the liver transcriptomes of fish reared at high water temperature across generations but with different temperature increments. Shows that stepwise temperature increase can change the way fish acclimate to end-of-the-century water temperatures.

**Bogan, S. N., M. E. Strader, and G. E. Hofmann. 2023. Associations between DNA methylation and gene regulation depend on chromatin accessibility during transgenerational plasticity. *BMC Biology* 21:149.**

Uses measurements of the gene expression and DNA methylation during the gametogenesis and embryogenesis of the purple sea urchin to provide evidence that DNA methylation can play pivotal roles during transgenerational plasticity, but also postulates that DNA methylation is only one epigenetic mechanism that is important for this process.

**Putnam, H. M., J. M. Davidson, and R. D. Gates. 2016. Ocean acidification influences host DNA methylation and phenotypic plasticity in environmentally susceptible corals. *Evolutionary Applications* 9.9: 1165–1178.**

Compares the epigenetic landscapes of two coral species, one more susceptible to ocean acidification than the other, and suggests that the different sensitivity to ocean acidification in the two coral species is controlled by an epigenetic reprogramming centered on DNA methylation.

**Ryu, T., H. D. Veilleux, J. M. Donelson, P. L. Munday, and T. Ravasi. 2018. The epigenetic landscape of transgenerational acclimation to ocean warming. *Nature Climate Change* 8.6: 504–509.**

Uses genome-wide bisulfite sequencing to measure the differentially methylated genomic landscape of coral reef fish reared at current day versus future water temperatures, and shows that selective DNA methylation of specific loci is a potential mechanism that parents use to transfer the information of the new environment to the next generation, facilitating acclimation to the ocean warming.

**Veilleux, H. D., T. Ryu, J. M. Donelson, et al. 2015. Molecular processes of transgenerational acclimation to a warming ocean. *Nature Climate Change* 5.12: 1074–1078.**

Uses genome-wide transcriptomic measurements to identify molecular pathways that underlie the ability of transgenerational fish to acclimate to ocean warming. Is able to show that metabolic pathways in the liver of fish acclimated to higher temperatures were differentially expressed compared to control fish.

## Metapopulations and Gene Flow

Evidence of fish metapopulations and possible gene flow under future climate conditions is reported in Schunter, et al. 2018. This study shows that changes in the brain transcriptome of fishes can explain their tolerance to elevated CO<sub>2</sub>. Similarly, Kang, et al. 2022 uses volcanic CO<sub>2</sub> seeps as natural analogues of future ocean acidification conditions, and shows that certain species of coral reef fishes displayed an accelerated evolution of genes involved in the response to a high-CO<sub>2</sub> environment. Although this can be seen as a positive outcome, we need to be careful because we cannot yet grasp the full extent of the impacts of climate change on entire ecosystems.

**Kang, J., I. Nagelkerken, J. L. Rummer, et al. 2022. Rapid evolution fuels transcriptional plasticity to ocean acidification. *Global Change Biology* 28.9: 3007–3022.**

Uses transcriptome measurements in the brain of five coral reef fish species collected at a natural volcanic CO<sub>2</sub> seep and compares these to those of fish collected at a control site. Shows that some of the differentially expressed genes in those fish living at the CO<sub>2</sub> seep have an accelerated evolution.

**Schunter, C., M. J. Welch, G. E. Nilsson, J. L. Rummer, P. L. Munday, and T. Ravasi. 2018. An interplay between plasticity and parental phenotype determines impacts of ocean acidification on a reef fish. *Nature Ecology & Evolution* 2:334–342.**

By measuring the genome-wide changes in gene expression in the brain of a coral reef fish, it is shown that parental phenotype can dictate the ability of offspring to acclimate to more acidic water.

## Marine Protected Areas and Conservation

The potential of marine protected areas to buffer the impact of climate change on fishes has been the focus of much research, yet it remains controversial. Roberts, et al. 2017 highlights how marine protected areas can help adaptation to multiple aspects of climate change (e.g., acidification, sea-level rise), including through rebuilding large fish populations and stocks that can further benefit nutrient cycling and carbon sequestration. Bates, et al. 2019 reviews the mechanisms by which marine protected areas are likely to enhance fish resilience to climate stressors, concluding that evidence of increased resistance to climate stressors in marine protected areas is currently limited. Bruno, et al. 2018 shows that under a business-as-usual scenario, global warming will cause further fish biodiversity losses in tropical and low-latitude marine protected areas. However, Bates, et al. 2014 demonstrates that marine protected areas can buffer fluctuations in temperate fish biodiversity and reduce fish tropicalization in a global warming hot spot. Frid, et al. 2023 highlights that the capacity of marine protected areas to harbor higher fish biomass persists across a broad temperature range. On tropical coral reefs, Mellin, et al. 2016 shows that protection from fishing can increase resilience to cumulative disturbance impacts from coral bleaching, tropical cyclones, and pest outbreaks. More research is required on the benefit of marine protected areas for estuarine fish species.

**Bates, A. E., N. S. Barrett, R. D. Stuart-Smith, N. J. Holbrook, P. A. Thompson, and G. J. Edgar. 2014. Resilience and signatures of tropicalization in protected reef fish communities. *Nature Climate Change* 4.1: 62–67.**

Quantifies the species richness, diversity, and functional traits of temperate fish communities over twenty years of warming in marine protected areas and fished sites within a global warming hot spot (Tasmania, Australia). Shows greater stability in fish biodiversity, recovery of large bodied-species, and resistance to tropicalization within protected areas.

**Bates, A. E., R. S. C. Cooke, M. I. Duncan, et al. 2019. Climate resilience in marine protected areas and the “Protection Paradox.” *Biological Conservation* 236:305–314.**

Reviews the biological and ecological mechanisms by which marine protected areas are expected to promote fish community resilience to climate stressors. Concludes that, when detected, the benefit of marine protected areas is relatively small against a backdrop of natural variability. Highlights the “Protection Paradox” as a possible reason, whereby protection from fishing can select for species that are highly sensitive to other stressors, including climate change.

**Bruno, J. F., A. E. Bates, C. Cacciapaglia, et al. 2018. Climate change threatens the world’s marine protected areas. *Nature Climate Change* 8.6: 499–503.**

Projects future sea surface temperature and oxygen concentration expected under a business-as-usual scenario (RCP 8.5) for the global ocean. Shows that temperatures that most fish species can tolerate will be exceeded by 2050 in the tropics and by 2150 for many higher-latitude marine protected areas.

**Frid, O., S. Malamud, A. Di Franco, et al. 2023. Marine protected areas’ positive effect on fish biomass persists across the steep climatic gradient of the Mediterranean Sea. *Journal of Applied Ecology* 60.4: 638–649.**

Used a 3,300 km natural temperature gradient across fifty-two rocky reefs in the Mediterranean Sea to study effects on fish communities. Finds an association between temperature increase and decrease in fish biomass and shifts toward more warm-affiliated species, respectively. Shows that these responses to elevated temperatures were also present in marine protected areas (compared to nonprotected areas).

**Mellin, C., M. A. MacNeil, A. J. Cheal, M. J. Emslie, and M. J. Caley. 2016. Marine protected areas increase resilience among coral reef communities. *Ecology Letters* 19.6: 629–637.**

Assesses the resilience of coral reef fish communities to cumulative disturbance impacts from tropical cyclones, coral bleaching, and pest outbreaks over a twenty-year time series on Australia’s Great Barrier Reef. Shows that reef fish communities within marine protected areas were more resistant to cumulative disturbance and recovered faster than those on fished sites.

**Roberts, C. M., B. C. O’Leary, D. J. McCauley, et al. 2017. Marine reserves can mitigate and promote adaptation to climate change. *Proceedings of the National Academy of Sciences of the United States of America* 114.24: 6167–6175.**

Reviews and discusses evidence for the potential benefit of marine protected areas to buffer multiple impacts of climate change, such as ocean acidification, sea-level rise, storm intensification, shifts in species distributions and reduced productivity and oxygen availability. Shows that by promoting large fish populations and stocks, marine reserves can also improve nutrient cycling and sequestration and buffer against environmental fluctuations.

## Biogenic Habitat Modification

Climate stressors can have strong direct effects on fishes, but the indirect effects via alterations to biogenic habitat can be as important. Ocean warming, for example, can lead to loss of kelp and coral habitats, with negative consequences on associated fish communities, as shown in Wernberg, et al. 2016 and Graham, et al. 2006. Elevated CO<sub>2</sub> can boost weedy turf algal growth and reduce the abundance of calcareous reef builders (e.g., corals, mussels, oysters) as well as non-reef builders (e.g., kelp), as shown in Nagelkerken and Connell 2022, which reshuffles fish communities and can reduce fish diversity, as shown in Nagelkerken, et al. 2017 and Cattano, et al. 2020. Warming further leads to range extensions of (sub)tropical fishes in temperate ecosystems, including herbivores that overgraze kelp forests and prevent their recovery, as shown in Wernberg, et al. 2016. Ocean acidification, however, can slow down the tropicalization of temperate environments by some tropical fishes by reducing urchin overgrazing on kelp, as shown in Coni, et al. 2021. Stuart-Smith, et al. 2021 shows that habitat generalist fish species are favored in areas where coral and kelp habitat has been lost.

**Cattano, C., S. Agostini, B. P. Harvey, et al. Changes in fish communities due to benthic habitat shifts under ocean acidification conditions. *Science of the Total Environment* 725:138501.**

Used a natural volcanic CO<sub>2</sub> vent in Japan to study the effect of habitat alterations on fish communities. Found that under elevated CO<sub>2</sub>, biogenic habitat shifted from structurally complex coral- or kelp-dominated habitats to low-relied turf-dominated systems. Observed a shift in fish community structure as well as reduced fish abundances and species diversity at the vents.

**Coni, E., I. Nagelkerken, C. M. Ferreira, S. D. Connell, and D. J. Booth. 2021. Ocean acidification may slow the pace of tropicalization of temperate fish communities. *Nature Climate Change* 11:249–256.**

Studied a natural warming hot spot in Australia and a volcanic CO<sub>2</sub> vent in New Zealand to evaluate the effects of biogenic habitat shifts on associated fish communities. Shows that the expansion of kelp-overgrazing sea urchins under ocean warming might be mitigated by the negative effects of ocean acidification on calcifying urchins. The reduced kelp grazing by urchins and the boost of turf algal growth under elevated CO<sub>2</sub> both facilitate a regime shift from barren rocky habitat to turf-dominated habitat, which is less favored by tropical range-extending fish species.

**Graham, N. A. J., S. K. Wilson, S. Jennings, N. V. C. Polunin, J. P. Bijoux, and J. Robinson. 2006. Dynamic fragility of oceanic coral reef ecosystems. *Proceedings of the National Academy of Sciences of the United States of America* 103.22: 8425–8429.**

Authors studied a coral reef in Seychelles that underwent a regime shift from a coral-dominated to a rubble- and algae-dominated state due to a severe coral bleaching event. They observed a concurrent local extinction of some fish species, reduced abundances of other fishes that relied on coral, and loss of species in key functional groups of fishes. They show that the loss of reef structural complexity was the main driver of loss of fish diversity.

**Nagelkerken, I., and S. D. Connell. 2022. Ocean acidification drives global reshuffling of ecological communities. *Global Change Biology* 28:7038–7048.**

Performed a global quantitative analysis of biogenic habitat change under ocean warming and acidification, based on studies performed at volcanic CO<sub>2</sub> vents and large mesocosms. Found consistent effects of community reshuffling (including fishes), but disparate effects on biodiversity and abundances.

**Nagelkerken, I., S. U. Goldenberg, C. M. Ferreira, B. D. Russell and S. D. Connell. 2017. Species interactions drive fish biodiversity loss in a high-CO<sub>2</sub> world. *Current Biology* 27.14: 2177–2184.**

Studied a natural volcanic CO<sub>2</sub> vent in New Zealand to evaluate the effects of biogenic habitat shifts on associated fish communities. Found that under elevated CO<sub>2</sub>, kelp-dominated systems changed in turf-dominated systems where fish diversity was reduced and the fish community showed homogenization through dominance of a single species. Increased food abundance and predator relief on this competitively dominant species is proposed as a mechanism for its numerical increase at the vents.

**Stuart-Smith, R. D., C. Mellin, A. E. Bates, and G. Edgar. 2021. Habitat loss and range shifts contribute to ecological generalization amongst reef fishes. *Nature Ecology and Evolution* 5:656–662.**

Used a global fish data set of tropical and temperate reef fishes and calculated their habitat niche breadth. Shows that tropical fishes that are habitat generalists are better at extending their ranges to higher latitudes under climate change than habitat specialists. Additionally, generalist species are favored above specialists in areas where coral or kelp habitat was lost.

**Wernberg, T., S. Bennett, R. Babcock, et al. 2016. Climate-driven regime shift of a temperate marine ecosystem. *Science* 353.6295: 169–172.**

Studied the macro-scale effects of an extensive and prolonged heatwave on temperate rocky reef systems in Australia. Found that due to the heatwave, kelp was replaced by turfs and abundance of tropical and subtropical seaweeds, invertebrates (including corals), and fishes increased at temperate latitudes. Years after the heatwave, kelp recovery was minimal, likely due to the increased abundance of kelp-eating tropical herbivorous fishes.

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