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REPORT

Fish services to corals: a review of how coral-associated fishes benefit corals

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Abstract On coral reefs, hard corals (order Scleractinia) provide habitat for an extraordinary diversity of reef fishes, many of which have close associations with the coral. Coral can provide these fishes nesting sites, food and protection from predators. The fishes can also benefit the corals, through fish-derived services resulting from, for example, diurnal and nocturnal movements, foraging, and nutrient excretion. Here, we synthesize how coral-associated fishes (i.e., coral reef fishes that have prolonged or permanent dependency on live coral) positively contribute to the health and resilience of corals. We highlight how certain coral-associated fishes offer a variety of benefits to corals, including enhanced oxygenation, nutrient subsidies and recycling, sediment removal, and protection against predators and parasites. Our review highlights the critical role that some coral-associated fishes have in supporting reef function, and in some cases, conferring resilience.

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Introduction

Despite occurring in nutrient-poor tropical waters, coral reefs are among the most diverse ecosystems globally (Reaka-Kudla et al. 1996; Plaisance et al. 2011). The exceptional biodiversity of these ecosystems can be attributed not only to the immense diversity of coral species, but also to the multitude of fish and invertebrate species that depend on these individual colonies, coral reefs, and the resources they provide (Bellwood et al. 2017; Siqueira et al. 2023). However, these coral reef ecosystems are facing increasing threats from a range of disturbances (e.g., pollution, overfishing, and climate change), causing the widespread destruction of the world's coral reefs (Eddy et al. 2021). The importance of hard corals to their fish and invertebrate occupants is evident; loss of coral quantity, quality, and/or complexity can affect fish and invertebrate biodiversity, abundance, and species composition (Beukers and Jones 1997; Jones et al. 2004; Bonin et al. 2011; Stier et al. 2014; Pratchett et al. 2020). There is also growing recognition of the reciprocal benefits that fishes and invertebrates offer to these corals (Stier and Osenberg 2024a). Such benefits may help buffer corals against natural and human-induced stressors, enhancing their resilience to changing environmental conditions (Toby Kiers et al. 2010). Comprehending these symbiotic relationships and their effects on coral biology not only deepens our understanding of the mutualistic networks that may have sustained coral reefs historically, but also offers insights into harnessing these positive interactions to enhance restoration efforts on reefs (Shaver and Silliman

2017; Ladd et al. 2018; Seraphim et al. 2020; Shaver et al. 2022).

In this paper, we focus on the positive effects of coral-associated fishes, which we define as species that maintain close spatial relationships with live coral structures, using them for shelter, feeding, breeding, or territorial defense. These associations range from obligate coral dwellers, which spend nearly their entire life within coral colonies such as damselfishes and gobies, to facultative species that use corals opportunistically or for shelter such as grunts and snappers (Fig. 1). Territorial species like farmerfish also interact with corals by colonizing live corals and then cultivating algae within their territories, which leads to the demise of some corals but facilitation of others (White and O'Donnell 2010). We highlight the multifaceted ways coral-associated fishes positively affect corals including: enhancing oxygenation, nutrient cycling, sediment removal, and predator defense, and mitigating the deleterious effects of disease, parasites, and macroalgae (Fig. 2). We then examine how these fish-mediated effects may interact with and potentially alleviate the harmful impacts of marine heatwaves. Lastly, we emphasize the need for a more mechanistic understanding of these fish-coral relationships, and discuss their implications for the conservation and restoration of coral reef ecosystems.

Fish-derived services to the coral holobiont

Below, we briefly review the major ways in which fishes can benefit the coral holobiont. We emphasize the coral holobiont because many of the proposed mechanisms by which fish benefit corals are mediated through effects on their symbiotic algae or their microbiome, rather than being limited to effects on the coral tissue only. We also emphasize beneficial effects instead of direct deleterious effects (like consumption of coral tissue), and we do not discuss indirect effects of herbivores on corals via reductions in macroalgal biomass, as these interactions are not directly tied to coral-fish interactions and have been covered extensively in other reviews (Ledlie et al. 2007).

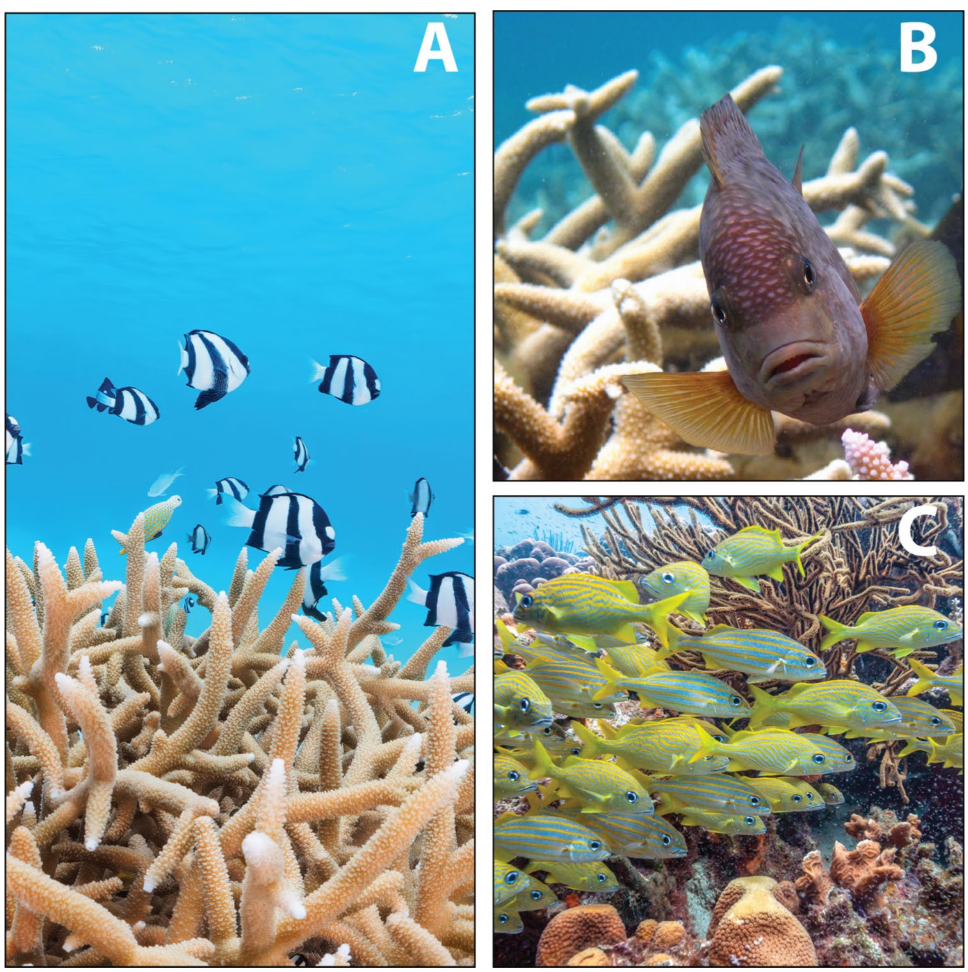

Fig. 1 Examples of coral-associated fishes and corals, including (**a**) damselfishes (*Dascyllus arunaus* and other species) and their host coral, *Acropora sp.*, in Okinawa, and **b** farmerfish (*Stegastes nigricans*) defending its territory of turf algae lawns with scleractinian corals, **c** diurnal aggregations of *Haemulon flavolineatum* (grunts) in the Caribbean (Photos: Adobe Stock)

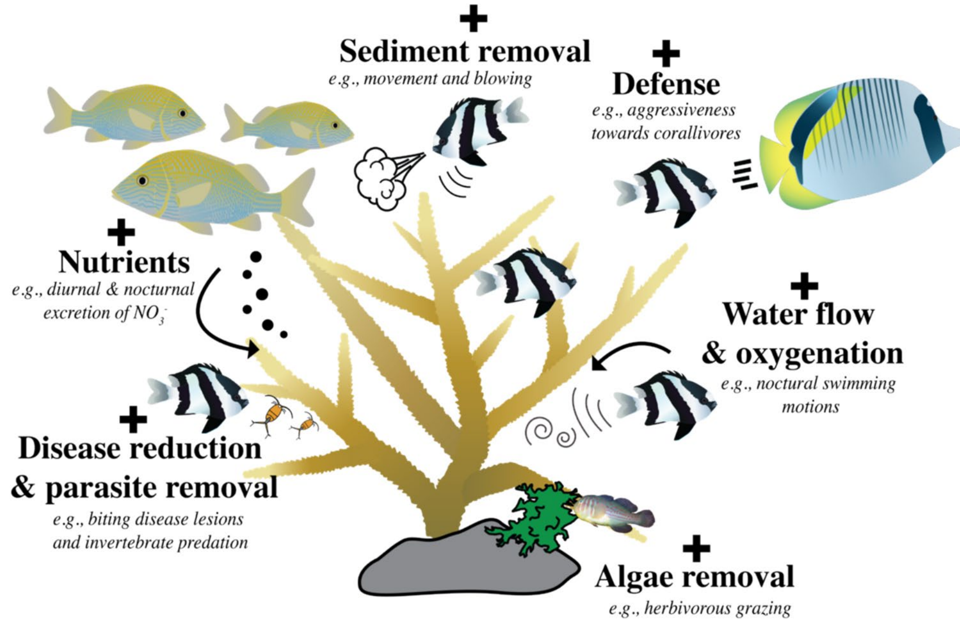

Fig. 2 Positive interactions between coral-associated fishes and their coral hosts. Coral-associated fishes provide several ecosystem services, including sediment removal, defense against coral predators, enhancement of water flow and oxygenation, nutrient cycling, algae removal, and reduction of diseases and parasites. These services directly support coral health by improving growth, reducing stress, and increasing resilience to environmental disturbances. Graphics from the Integration and Application Network (ian.umces.edu/media-library)

Oxygenation and water flow

Coral-associated fishes may play a key role in oxygenating and increasing water flow around the surface of branching corals which is vital to the metabolism of corals and their symbiotic algae (Nelson and Altieri 2019). This process may be particularly key at night, when the center of a branching coral can become anoxic due to a lack of water flow, in combination with respiration by the coral in the absence of photosynthesis by Symbiodiniacea (Shashar et al. 1993). An early study Goldshmid et al. (2004) initially discovered ventilation by three coral-associated fishes: *Dascyllus marginatus*, *Dascyllus aruanus*, and *Chromis viridis*. Two additional studies provide key insights into the effects of this oxygenation on coral biology. For example, Berenshtein et al. (2015) studied the contribution of damselfishes to coral oxygenation at night. These fishes, while largely inactive during the night, continue to hover in a sleep-like state within the coral matrix. This activity maintains a continuous flow of water across the coral surface, enhancing gas exchange, reducing the diffusive boundary layers and thereby improving oxygenation of the coral (Goldshmid et al. 2004; Berenshtein et al. 2015). Beneficial effects of fish-induced water movement are also apparent during the day: e.g., Garcia-Herrera et al. (2017) found that one of these same coral-dwelling damselfish *Dascyllus marginatus* increased coral photosynthesis by 3–6% via fish ventilation. This body of work is particularly relevant to corals of today and the future because hypoxia is increasing on many coral reefs, which can have devastating effects on corals and their occupants (Altieri et al. 2017; Hughes et al. 2020; Pezner et al. 2023), and fishes can help mitigate those effects.

Nutrient cycling and subsidy

Reef fishes provide concentrated nutrients to corals by foraging in the water column or on the seafloor, and then returning to shelter in the coral reef, where they egest and excrete nutrients (Allgeier et al. 2017). Fish excretion and feces provide macro- and micro-nutrients, although the composition and concentration of these nutrients vary among fish species and trophic guilds (Van Wert et al. 2023). Ammonium (NH_4^+), which is the most readily available form of nitrogen for the coral holobiont, is one of the most important nutrients excreted by fishes (Allgeier et al. 2017). Fish excretion increases the availability of ammonium to the coral and its Symbiodiniacea (Shantz et al. 2023) affecting reef biogeochemical cycles and increasing coral growth (Allgeier et al. 2017). Early work on large schools of grunts (Haemulidae) in the Caribbean showed that grunts foraged away from reefs at night, but hovered near and around corals during the day (Meyer et al. 1983; Meyer and Schultz 1985a, b). These migrating fish schools provided essential nutrients (including nitrogen and phosphorus) to corals, which enhanced the density of Symbiodiniacea and consequently increased coral growth (Meyer et al. 1983; Meyer and Schultz 1985a, b).

More recent work has shown that these grunt shoals increase the concentration of nitrogen and phosphorus around corals by tenfold, causing increases in crustose coralline algae but reductions in macroalgae, and leading to a 75% increases in growth of *Acropora cervicornis* (Shantz et al. 2015). The reduction in nutrient-limited macroalgae was not predicted, but reefs occupied by schools of grunts had substantially higher rates of grazing by herbivores, which mitigated any potential benefit of nutrient addition on the macroalgae. The net beneficial effects of grunts has the potential to facilitate coral recovery after disturbance events. However, surveys at larger scales in the Florida Keys found an entirely different pattern, with lower rates of herbivory, lower abundance of juvenile corals, and higher macroalgae biomass in areas with higher amounts of fish excretion (Burkepile et al. 2013). Thus, it is possible that either there is a paradox with differing patterns arising at different spatial scales, or that there are alternate stable states, such that once a reef tips into an algal dominated state, fish excretion facilitates further overgrowth of coral by algae (Mumby 2009).

Effects of coral-associated fishes on corals can also extend to reproductive benefits as demonstrated by studies of the damselfish, *Dascyllus marginatus*, and its host coral, *Stylophora pistillata*, in the Gulf of Eilat (Liberman et al. (1995). Over a 13-month period, corals with resident damselfish exhibited approximately 37% greater growth in skeletal surface area compared to corals without fish. While there was no change in per surface area reproductive output, corals with fish did have higher reproductive capacity due to their greater surface area.

Complementary studies in the tropical Pacific provide important insights into the temporal variation in benefits and how these benefits vary with coral morphology. For example, growth of the branching coral, *Pocillopora* sp. was positively associated with densities of damselfishes (*Chromis viridis*, *Dascyllus aruanus*, and *Dascyllus flavicaudus*) living inside the coral colonies (Holbrook et al. 2008). Ammonium in the interstitial spaces of the coral was elevated, especially during midday when fish feeding peaked, and also at night when the planktivorous fishes were sheltering within the coral. Characteristics of the coral influenced the magnitude of these effects. For example, another species of *Pocillopora* with a wider branching pattern (*P. grandis*) had much lower retention times of ammonium compared to the narrow branching corals (Holbrook et al. 2008), demonstrating an interaction between the effects of fishes and coral morphology.

The role of coral-associated fishes in affecting coral growth also can depend on the environment. *Dascyllus aruanus* can ameliorate the negative effects of depth and low light on growth of *Pocillopora damicornis* (Chase et al. 2014), but these positive effects flipped to negative effects in sites with high nitrogen concentrations and high flow (Chase et al. 2014). While the mechanism of these context dependencies remains somewhat unclear, a recent dynamic energy budget model by Detmer et al. (2022) showed that the positive effects of fishes on corals could switch to negative at very high densities of fish due to the very high nitrogen concentrations: nitrogen can be beneficial at low concentrations, but may be deleterious or toxic at higher concentrations (Gil 2013; Becker et al. 2021; Detmer et al. 2022). Exactly how the concentrations of water column nitrate or ammonium concentrations and fish interact is an active area of research. Only one study to date has factorially manipulated fishes and background nutrients. On an artificial reef in the Bahamas, Allgeier et al. (2020) manipulated nutrients and fish, and examined how coral growth and the density of Symbiodiniacea changed. Fish effects did not depend on the addition of nitrogen; however there also was no main effect of nitrogen, suggesting that the concentration of nitrogen was only minimally affected by the nitrogen addition treatment and was not sufficiently high to create deleterious effects of fish.

Sedimentation

The presence of fishes within the coral colony not only reduces anoxia and increases nutrients, but can also lead to the removal of sediments. Because sediments can reduce coral survival by reducing light availability, heterotrophic feeding, and oxygen availability (Weber et al. 2012), fishes can enhance coral survival, especially in coastal areas with high sediment loads. For example, in experiments with the damselfish, *Dascyllus aruanus* and *Pomacentrus moluccensis*, corals without fish had 2–5 × more sediment accumulation compared with colonies with fishes, resulting in up to a 90% reduction in coral survival (Chase et al. (2020b). Coral dwelling fishes can remove sediments from coral via passive means (i.e., by their movement within and around host corals), by stimulating coral mucus production (i.e. which can lead to sediment removal), by movement of coral polyps (which can also dislodge sediments) (Stafford-Smith and Ormond 1992) or via consumption or trapping sediments in their gills (Chase et al. 2020b). Because these same fishes provide nutrients to the coral, which likely increases the energy available for mucus production or polyp movement, the effects of fish on sediment removal and the supply of nutrients likely interact synergistically.

Protection from corallivores

Coral-associated fishes can mitigate the negative effects of coral predators by defending their colony from predation (Dirnwoeber and Herler 2013). For example, *Dascyllus aruanus* reduced the feeding rate of butterflyfishes on *Pocillopora damicornis* colonies by 90% (Chase et al. 2014, 2018). *Stegastes nigricans*, a territorial farmerfish that farms turf algae and is common to the South Pacific, protects branching coral colonies within its territory from a suite of corallivorous fishes (e.g., *Arothron meleagris* and *Chaetodon lunulatus*). Surveys of similar farmerfish territories in Guam and Polynesia have shown that coral diversity is much higher inside when compared to outside territories (Shannon's diversity index (H′) = 0.52 (inside) and 0.14 (outside)); some coral species (n = 3) are only found within *Stegastes* territories (Gochfeld 2010). Colonies of *Acropora striata* and *Montipora floweri* in French Polynesia had higher growth and survival rates inside *S. nigricans* territories compared to reefs without these territorial fishes (Gleason 1996; White and O'Donnell 2010). Similar studies in Guam found that tissue loss of *Pocillopora damicornis* was reduced by 50% in farmerfish territories compared to outside the territories (Gochfeld 2010). The most aggressive groups of *S. nigricans* (groups with more large fish) had the biggest beneficial effects on the growth and survival of branching corals (Pruitt et al. 2018; Kamath et al. 2019). Similarly, *Acanthocromis polyacanthus*, defended their host corals against predation by the crown of thorns seastar (*Acanthaster planci*) by nipping at the seastar's tube feet (Weber and Woodhead 1970). Additionally, some planktivorous damselfishes consume *Acanthaster* seastar larvae (Cowan et al. 2016), which may reduce the subsequent density of these voracious predators, although evidence for this mechanism remains untested.

Coral disease and parasites

At least ten coral-associated fish species (e.g., farmerfishes, damselfishes, blennies, and butterflyfishes) are known to enhance the survival of corals by biting at or consuming diseased patches of coral tissue, which can slow the progression of disease or completely eliminate it (Cole et al. 2009). For example, butterflyfish in the field and lab directly bite at lesions caused by black-band and brown-band disease, reducing the amount of diseased tissue on the coral host (Chong-Seng et al. 2011). While this behavior may benefit corals, other research suggests that corallivorous fish, can act as vectors of disease (see review by Renzi et al. 2022), potentially negating the beneficial effects. That said, the butterflyfish, *Chaetodon plebeius*, feeding on diseased coral tissue did not transmit these pathogens directly, while the snail, *Drupella,* did (Nicolet et al. (2018). This disparity likely occurred because their feeding scars of the fish are relatively shallow and fail to penetrate deeply enough into coral tissue to create an entryway for pathogens, while *Drupella* leave deeper feeding scars that significantly increase the risk of pathogen transmission. Similar variation in feeding by different species of fishes (e.g., butterflyfish vs. pufferfish) may drive variation in determining if fish protect corals from their pathogens or facilitate their transmission.

Coral-associated fishes can reduce the abundance of coral macro-parasites, such as harpacticoid copepods, which can suppress coral health, weaken colony structure, and deplete nutritional supplies (Barton et al. 2020).. For example in the South China Sea, an *Acropora*-associated goby, *Gobiodon quinquestrigatus*, consumes a variety of invertebrates associated with the host coral, approximately 25% of which were coral parasites (Zikova et al. 2011). These parasites included crustaceans such as Ascothoracida and Siphonostomatoida, as well as larvae of parasitic isopods and Facetotecta. While it is unclear how much fish reduce the density of coral parasites, or the consequences for coral health, these studies suggest that fish have the potential to benefit corals by controlling their parasites. This possibility warrants further attention.

Coral-algae interactions

Although we do not review indirect effects of herbivory on corals (see Nash et al. 2016 for a recent review), there are some notable cases in which removal of algae by some coral-associated fishes deter the growth of harmful algae and create an environment less conducive to algal proliferation. In turn, this reduction in algae can limit the negative effects of algae on coral growth and survival. For example, Dixson and Hay (2012) provided a critical examination of the interactions among the coral, *Acropora nasuta*, two gobies, *Gobiodon histrio* and *Paragobiodon echinocephalus*, and a toxic seaweed, *Chlorodesmis fastigiata*. When the coral comes into contact with the toxic seaweed it emits a chemical signal that attracts the gobies to the affected area. The gobies then trim the seaweed to eliminate contact with the coral and thus mitigate potential damage to the coral. The two goby species display very different behaviors, which results in different consequences for the fish. For instance, *Paragobiodon echinocephalus* removes the seaweed without ingestion, as might be expected because *Chlorodesmis* is toxic. However, *Gobiodon histrio* not only removes the seaweed, but also consumes it without any apparent harm, thereby increasing its own toxicity. The toxicity of the fish provides a defensive benefit against its predators (Gratzer et al. 2015). Thus, both the coral and the fish derive reciprocal benefits, which underscores the sophistication of interspecies communication within coral reef ecosystems, and the importance of documenting key symbioses integral to the stability and health of these habitats. Such interspecific interaction may be more prevalent than previously thought. For example damselfishes consume and/or remove filamentous algae from bleached coral colonies, which reduced further algal colonization of these vulnerable corals (Chase et al. 2020a).

Fish benefits during marine heatwaves

The benefits provided by coral-associated fishes appear particularly valuable during marine heatwaves, which are increasing in frequency and intensity due to climate change (Frölicher et al. 2018). Research from the Great Barrier Reef and Moorea demonstrates that coral-associated fishes can significantly enhance coral performance under thermal stress (Chase et al. 2018; Shantz et al. 2023). In laboratory simulations of heatwaves (short periods at ~ 32 °C), corals harboring damselfish maintained higher *Symbiodinium* densities, and sustained robust physiological functions, and continued growth compared to corals without fishes (Chase et al. 2018; Shantz et al. 2023). This resilience is largely attributed to the altered nutrient dynamics facilitated by the fish, especially through the steady excretion of ammonium. Ammonium availability, which increased 2.20 µM when fish were present, likely facilitates higher levels of photosynthetic efficiency (Fv/Fm) and protein content in corals, critical for combating oxidative stress during thermal events (Ezzat et al. 2015; de Barros et al. 2020; Shantz et al. 2023).

However, field studies during prolonged, intense heatwaves (temperatures exceeding 32 °C for over four weeks) revealed that, while corals with fishes initially showed fewer symptoms of bleaching, over 95% eventually succumbed to thermal stress and mortality, illustrating the limits of fish-provided resilience under extreme conditions (Chase et al. 2018). These findings highlight that, while fish-derived nutrients, particularly ammonium, support coral resilience by stabilizing Symbiodiniaceae populations and enhancing energy reserves, these benefits may only mitigate but not entirely prevent coral mortality under severe, sustained heatwaves. Together, this research underscores the critical role of coral-associated fishes in providing immediate resilience to thermal stress, though their long-term effectiveness may be constrained as marine heatwaves become more prolonged and intense.

Other fishes may also indirectly increase coral resilience to heat stress by reducing predation on the coral. The territorial farmerfish *Stegastes nigricans* significantly lowered mortality rates and enhanced recovery of corals within their territories during heatwaves (Suefuji and van Woesik 2001; Honeycutt et al. 2023). While nutrients supplied by the *Stegastes* is one possible explanation, Honeycutt et al. (2023) suggested that decreased coral predation might provide another mechanism that explains reduced mortality if confronted with heat stress. When protected by farmerfish, corals contracted their polyps less frequently, which increased their ability to feed on zooplankton (Honeycutt et al. 2023). This additional heterotrophic nutrition helps the coral survive, especially if a heatwave impairs the coral-Symbiodiniacea symbiosis (Grottoli et al. 2006; Houlbrèque and Ferrier-Pagès 2009).

Indirect effects

In coral reef ecosystems, fish-coral interactions are embedded within a web of interactions, which can have indirect effects on the coral. For example, damselfish (*Dascyllus flavicaudus*) shelter within branching corals such as *Pocillopora eydouxi*, enriching the coral with nitrogenous waste that enhances growth through nutrient input to its symbiotic algae (Holbrook et al. (2011)). As the coral grows, it supports higher densities of damselfish, strengthening the mutualistic feedback which benefits the fish and coral. This mutualistic loop is sensitive to interactions with other coral-dwelling fish, such as hawkfish (*Paracirrhites arcatus*), which prey on the damselfish, disrupt the feedback, and reduce the benefit the coral receives from the damselfish.

Moeller et al. (2023) examined how predators affect fish-coral mutualisms, focusing on the role of hawkfish. Although hawkfish consume damselfish and can therefore reduce the beneficial effects on corals (Holbrook et al 2011: see above), they also modulate competitive interactions within coral communities. In some cases, hawkfish predation may reduce the density of one type of mutualist, but enable competitively inferior but more beneficial mutualists to thrive. Similarly, different predator species can affect coral health by altering the diversity and abundance of coral-dwelling cryptofauna (Stier and Leray (2014), such as decapods (*Trapezia* spp.) that provide cleaning and defense services crucial for coral resilience (Stier and Osenberg 2024b). Coral-associated predators like the flame hawkfish (*Neocirrhites armatus*) and coral croucher (*Caracanthus maculatus*) decrease the abundance and diversity of these cryptofauna, likely indirectly reducing the coral's capacity to grow and survive (e.g., when exposed to coral predators or sedimentation).

Gaps in knowledge and future lines of research

This review highlights the important benefits that fishes can provide corals. However, there remain a wide diversity of unanswered questions. The answers to these questions will likely facilitate our understanding of the evolution of coral reef ecosystems, their response to a variety of stressors, and their resilience to disturbances. Below, we articulate five categories of research questions that we think are most important to answer in the coming decade.

(i) Elucidating Mechanisms of Fish-Mediated Coral Health Enhancement

While coral-associated fishes contribute to coral health through behaviors like sediment removal, nutrient augmentation, and the reduction of bioerosion, the mechanisms underlying many of these benefits are not well understood. Future research should aim to clarify these mechanisms. For example, how much of the effect of fishes on sediment removal is due to passive movement of the fish, active removal of sediments by the fish, or stimulation of processes the coral uses to dislodge sediments? Similarly, the beneficial effects of fish-derived nitrogen on the production of symbiotic algae can become deleterious to the coral host, although level at which this occurs is poorly understood, which impeded our ability to anticipate the environments in which fish will have positive vs. negative effects on corals.

Many of the benefits that accrue from coral-associated fishes arise from specific knowledge of the behavior (e.g., predator defense) and physiology (e.g., excretion rates) of the fishes, many of which unique to a subset of the fish community. Similarly, different corals (e.g., due to their morphology) will respond differently to the same fish associate. Future research should use controlled experiments and field studies to develop a "service catalog" that matches fish species with coral types to enhance coral resilience and guide targeted restoration strategies: e.g., to outplant particular coral taxa with specific fish species to maximize coral benefits. Of course, these benefits will only last as long as the coral and fish remain associated but given the life history of many of these fishes, this association could persist for several years, which may be sufficient to allow establishment of transplanted corals. Because some fishes demonstrate conspecific attraction (Sweatman 1985), the initial pairing of corals with fishes may persist over multiple generations.

(ii) Evaluating the Impact of Environmental Stressors on Fish-Coral Synergies

Environmental stressors—including rising sea temperatures, ocean acidification, eutrophication, hypoxia, and declining water quality—may modulate the benefits conferred by fishes to corals. As climate change exacerbates these stressors, understanding how the stressors interact with coral-associated fishes becomes critical. This knowledge will help predict the conditions under which fish can most effectively support coral resilience in changing oceans. Advanced techniques such as stable isotope analysis, metabolomics, and transcriptomics could illuminate how fishes influence coral metabolic pathways, energy allocation, and stress response mechanisms. Understanding these interactions at a molecular level may uncover novel targets for enhancing coral resilience. Initial evidence exists for coral-associated fishes to buffer the impact of anthropogenic stressors is evident at small scales. Certainly, none of the positive effects are likely to offset the tremendous effect of human-caused impacts on coral reefs, but there is hope that some of these fish-coral interactions might be harnessed to augment ongoing local scale restoration efforts (Ladd et al. 2018).

(iii) Investigating long-term dynamics of coral recovery with fish presence

This review has highlighted the short-term benefits of coral-associated fishes on corals. These benefits entail mechanisms (e.g., colony defense, enhanced water flow) that produce quantifiable increases in coral traits (e.g., Symbiodiniacea density, N and P content, photosynthetic efficiency) that ultimately translate into enhanced performance of the colony (e.g., calcification, growth, and survival) and potential population-level benefits (Fig. 3). Yet, the longer-term responses at the colony level as well as population-level effects are not well known. Do the short-term benefits persist over time or do they become more muted? Longitudinal studies are needed to determine whether corals hosting resident fish populations exhibit enhanced resistance and recovery across multiple disturbance events, such as successive bleaching episodes or storm impacts. Research should focus on quantifying metrics like growth rates, condition, reproductive success, and population dynamics in the presence of fish over extended periods, identifying thresholds

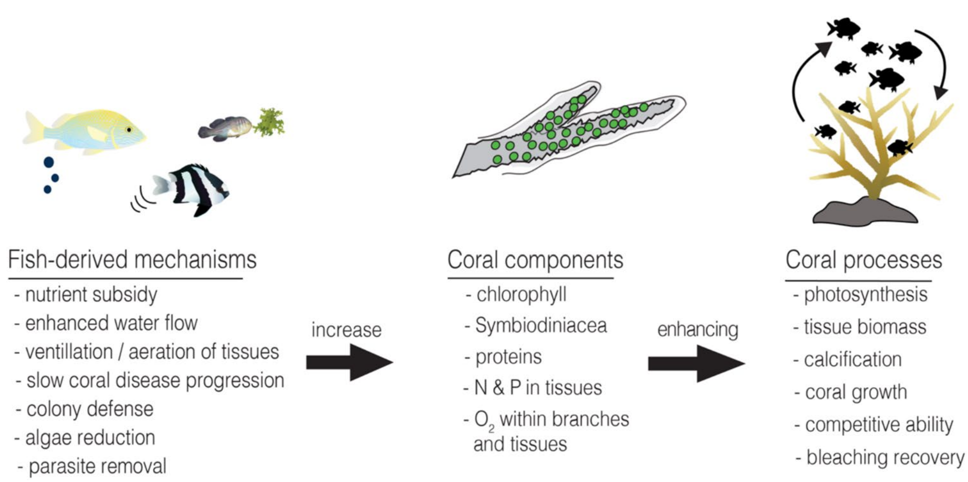

Fig. 3 Coral-associated fishes contribute to the health and function of corals. Fish-derived mechanisms, such as nutrient subsidies, enhanced water flow, tissue aeration, disease progression mitigation, colony defense, algae reduction, and parasite removal, increase key components of coral biology, including chlorophyll content, Symbiodiniaceae density, protein levels, nitrogen (N) and phosphorus (P) in tissues, and oxygenation within coral branches and tissues. These enhancements support critical coral processes, including photosynthesis, tissue biomass production, calcification, overall growth, competitive ability, and recovery from bleaching events. Arrows represent the progression from fish-mediated mechanisms to improved coral performance and resilience. Graphics from the Integration and Application Network (ian.umces.edu/media-library)

and tipping points critical for coral persistence under climate change scenarios.

(iv) Exploring Fish Influence on Coral Microbiomes and Holobiont Health

Fish may play a role in shaping the coral microbiome—a key determinant of coral health and immunity—through mechanisms such as nutrient cycling. Future studies employing metagenomic and metatranscriptomic approaches can compare microbial communities and their functions in corals with and without associated fish. Understanding how fish-mediated alterations in the microbiome affect coral stress responses and disease resistance could reveal indirect pathways through which fish bolster coral resilience, highlighting the importance of considering the coral holobiont in conservation efforts, possibly by inoculating corals with specific microbiomes that amplify beneficial effects of fishes.

(v) Integrating Benefits and Costs in Coral-Fish Interactions

We have described a suite of benefits fishes provide to corals. But we should remember that not all coral-associated fishes are beneficial. For example, tissue feeding by butterflyfish or bioerosion by certain parrotfish can reduce coral growth and facilitate the transmission of pathogens. Some species within putatively beneficial families can reduce coral growth: e.g., the damselfish, *Plectroglyphidodon johnstonianus*, feeds almost exclusively on coral (Ho et al. 2009). Even fish species known to have beneficial effects, can negatively affect corals under some environmental contexts. For example, damselfishes that recycle nutrients can have negative effects on corals in areas with high background levels of nitrate (Chase et al. 2014), and farmerfish can negatively affect nearby mounding corals (e.g., cultivating algae that overgrow the colony) even though these fish can positively affect branching corals (White and O'Donnell 2010). Currently, the net effect of these negative and positive interactions on corals remains uncertain. Future work should take this species and environment-specific knowledge and predict (and test) how effects are manifest by more diverse fish and coral communities: e.g., are effects additive or do diverse fish assemblages yield unexpected effects? Controlled experiments and large-scale field observations across varying environmental contexts can identify conditions under which these community-level effects are most beneficial and identify the environmental conditions under which the net effect of fishes shift from beneficial to detrimental. Such information can be used to inform management strategies that balance ecosystem functions with coral conservation goals.

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Declarations

Conflict of interests The authors declare no competing interests.

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