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Full length article Trophic interactions in coral reef restoration: A review

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A R T I C L E I N F O

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ABSTRACT

Ecology plays a central role in the management and conservation of ecosystems. However, as coral restoration emerges as an increasingly popular method of confronting the global decline of tropical coral reefs, an ecological basis to guide restoration remains under-developed. Here, we examine potential contributions that trophic ecology can make to reef restoration efforts. To do so, we conducted a comprehensive review of 519 peer-reviewed restoration studies from the past thirty years. From our review, we quantified how various important trophic interactions have been considered by restoration practitioners to date and discuss how they may be utilized to benefit coral restoration. We found that despite rapidly growing interest in coral restoration, only 15% of restoration publications considered trophic interactions, highlighting a clear mismatch between the fundamental role of trophic ecology on coral reefs and its consideration in restoration efforts. Herbivory was by far the most commonly studied process (46 publications) while other processes such as corallivory (17 publications), coral heterotrophy (8 publications), and consumer-derived nutrient cycling (4 publications) received far less attention despite their known importance on reefs. To promote consideration of these important processes in restoration, we consider how specific trophic interactions within each of these areas can be leveraged through direct and indirect pathways to benefit coral restoration. Ultimately, we argue that rather than considering important trophic interactions as emergent outcomes of reef restoration, practitioners utilize the lessons learned from trophic ecology to help achieve their desired restoration outcomes.

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1. Introduction

Coral reefs are iconic ecosystems well known for their biodiversity and beauty, and widely recognized for the invaluable societal, economic, and ecological services they provide (Moberg and Folke, 1999; Woodhead et al., 2019). For instance, reef fisheries land nearly 30,000,000 t of fish year⁻¹ (UNFAO, 2018) and at least 100,000,000 people world-wide benefit from coastal protection provided by barrier reefs (Ferrario et al., 2014). However, corals are rapidly dying around the globe. Caribbean reefs have lost more than 80% of their coral over the past four decades (Jackson et al., 2014), and after recent mass bleaching events many Indo-Pacific reefs are approaching similar levels of decline (Hughes et al., 2018, 2017). This accelerated and clear demise of coral reefs globally during the past half century endangers both the natural diversity of tropical reefs as well as the goods and services these ecosystems provide (Alvarez-Filip et al., 2013; Rogers et al., 2014; Woodhead et al., 2019).

In response to widespread reef degradation, coral restoration has emerged as a popular and well-publicized tool to combat reef decline.

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Early coral restoration projects often focused on transplanting corals from healthy reefs to areas impacted by small-scale disturbances, such as ship groundings, storms, or dredging (Rinkevich, 2005). Since then, contemporary coral restoration has scaled up dramatically and now primarily entails outplanting nursery-raised corals to degraded reefs (Young et al., 2012). This restoration method has become so popular that coral nurseries now exist in every tropical ocean basin, with over 150 restoration groups operating nurseries in the Caribbean alone (Lirman and Schopmeyer, 2016). Yet, despite the substantial time and resource investment, coral restoration efforts often overlook the fundamental ecology of coral reefs (Ladd et al., 2018; Shaver and Silliman, 2017). This failure to include the ecological principles that are central to shaping coral reef ecosystem function (Brandl et al., 2019) is a missed opportunity to capitalize on natural processes on reefs to improve the efficiency and outcomes of restoration efforts.

Ecology plays a central role in management and conservation by providing insight into the biotic and abiotic forces that organize and structure ecosystems (Clark et al., 2001; Peterson et al., 2003; Rogers et al., 2014). While restoration efforts can be traced back at least a century to the pioneering projects of Aldo Leopold, the past few decades have seen a concerted push to explicitly integrate ecological principles into restoration. Beginning with Palmer et al. (1997), who argued that community ecology should play a central role in ecological restoration,







the early years of the 21st century were marked by calls to utilize ecology to repair degraded terrestrial and marine ecosystems (*e.g.* Epstein et al., 2003; Miller, 2002; Yap, 2000). Today, terrestrial conservation and restoration efforts often leverage fundamental ecological processes, like herbivory and competition, to achieve restoration goals (Suding et al., 2004; Young et al., 2016). Similarly, in the marine realm, the guidelines for managing sustainable fisheries and establishing marine protected areas are often grounded in ecology (*e.g.* Pikitch et al., 2004; Balbar and Metaxas, 2019). However, while the restoration of many coastal and marine ecosystems has incorporated ecological principles and interactions into restoration designs (Bruno et al., 2003; Halpern et al., 2007; Silliman et al., 2015), coral restoration has been slow to embrace this framework.

On coral reefs, trophic ecology is fundamental to our understanding of how reefs are organized and sustained. Indeed, trophic interactions underpin many of the processes that drive coral reef community structure and the key ecological services these ecosystems provide (Brandl et al., 2019; Burkepile and Hay, 2006; Mcleod et al., 2019). For example, herbivores consume seaweeds and provide top-down forcing that decreases competition between corals and algae, thereby helping corals persist and recover from disturbances (Adam et al., 2011; Bellwood et al., 2004; Shantz et al., 2020). Similarly, high productivity on many tropical reefs is sustained by planktivorous fishes that link open ocean and benthic food webs (Morais and Bellwood, 2019), and migratory fishes that transport nutrients across and between habitats (Layman et al., 2011; Shantz et al., 2015). In turn, the rapid turnover of cryptobenthic fishes supports large communities of piscivores and higher trophic levels (Brandl et al., 2019). Thus, as the rapid demise of reefs drives unprecedented coral restoration efforts around the globe, it is important to understand how these trophic interactions, or their loss, influence restoration outcomes.

Here, we examine potential contributions of trophic ecology to coral restoration. We provide a comprehensive review of coral reef restoration literature to quantify how these pathways have been considered by restoration practitioners to date and how they have been applied to enhance restoration success. In doing so, our goal is not to provide an exhaustive review of trophic ecology on coral reefs but to highlight well studied components of coral reef food webs and their ability to influence restoration outcomes. We identify three general processes: (1) Consumptive effects of reef animals on corals, (2) Coral heterotrophy, and (3) Consumer-derived nutrient cycling; and discuss the potential roles that these processes can play in coral restoration. While we recognize that many other aspects of trophic ecology could be incorporated into coral reef restoration, our hope here is that these ideas provide immediate benefits to restoration efforts while encouraging others to consider how trophic ecology can facilitate the recovery of degraded coral reefs.

2. Literature review

To assess the trends in how trophic ecology has been included in coral restoration studies, we conducted a review of peer reviewed literature from 1901 to present in the full collection database of ISI Web of Science. Using the search term "coral" AND "restoration" we identified 1218 potential studies. Because our focus is on the restoration of tropical reef building corals we excluded all studies that did not specifically pertain to tropical reefs (e.g. mangrove, seagrass, and deep water reef restoration) as well as patents and non-peer reviewed literature such as letters and conference proceedings, leaving us with 519 studies. We divided these 519 studies into three broad categories: i) Ideas & Perspectives; ii) Experimental & Data Analyses; and iii) Reviews; and further classified their main areas of focus as they pertain to restoration (ecological, methodological, financial, or social). Finally, we examined whether the papers assessed any elements of trophic ecology on coral reefs, and if so, what aspect(s) of trophic ecology were investigated. The full list of studies, as well as detailed methods and our criteria for inclusion in each category and sub-category can be found in Supplemental Table 1.

2.1. Trends in coral reef restoration literature

Interest in coral restoration is growing rapidly in the research community and over half of the studies we identified were published within the past five years (Fig. 1). From the 519 suitable studies that we found, 368 explicitly examined coral reef restoration while 151 were not specifically targeted towards restoration but noted that portions of their findings were of potential importance for restoration. Of the studies that explicitly examined coral reef restoration, most publications were experimental or combined some element of experimental research with a literature review or prospectus. Papers that were strictly reviews or ideas comprised a small component of the literature. In experimental studies, there has been a gradual shift from mostly methodological- towards ecological-focused research (Fig. 1), suggesting a growing recognition of the important role ecology plays in successful restoration. Still, just 15% of studies have considered how trophic interactions can influence coral reef restoration (Fig. 2), emphasizing the need for greater consideration of trophic ecology in coral restoration efforts. Below, we review the major findings of these papers, discuss lessons learned to date, and identify critical knowledge gaps and future directions through which trophic ecology can facilitate successful coral reef restoration.

3. Herbivory, predation, and trophic cascades on tropical reefs

3.1. Herbivory

Coral reefs are biodiverse ecosystems with complex food webs (McMahon et al., 2016). Even on the relatively species-poor reefs of the tropical Eastern Pacific, nearly 300 interspecific links exist in the subweb of corals, coral eating animals, and their higher-level predators (Glynn, 2004). However, of all the trophic interactions on tropical reefs, herbivory is the most studied and is widely recognized as critical for maintaining coral dominated reefs (Randall, 1965; Sammarco et al., 1974; Lewis, 1986; Burkepile and Hay, 2006). Herbivores facilitate coral settlement, growth, and survival by consuming algae that compete with coral for space, transmit coral diseases, and poison coral tissue (Connell, 1997; Nugues et al., 2004; Rasher and Hay, 2010). Furthermore, herbivory is critical to limiting the proliferation of macroalgae after major disturbances so that corals can recolonize reefs (Adam et al., 2011; Holbrook et al., 2016). Thus, herbivores should be natural allies for restoration practitioners.

Indeed, out of all trophic interactions, herbivory has received the most attention to date from the restoration community (Fig. 2). Of the 81 publications we identified that included trophic interactions, 46 addressed herbivory (Supplemental Table 1). Roughly 40% of these papers (n = 19) were reviews, perspectives, or modelling studies. Eight studies focused on leveraging herbivory to facilitate coral propagation (i.e. growth and survival) in land-based (ex situ) and ocean-based field (in situ) nurseries, with seven out of eight reporting positive effects of herbivore inclusion. For example, Henry et al. (2019) found that including herbivorous snails in culture tanks improved the growth and survival of Caribbean staghorn coral (Acropora cervicornis). Similarly, growth and survival of Pacific staghorn (A. millepora) recruits was positively related to the density of juvenile herbivorous tuxedo urchins (Mespilia globulus) that they were raised with (Craggs et al., 2019). Field nurseries also tended to benefit from inclusion of herbivorous fishes through reduced fouling and cleaning time. In the only exception, Baria et al. (2010) found that caging coral recruits at a mid-water nursery to prevent fish access increased recruit growth and survival rates (see Corallivory below). Thus, with the exception of raising recruits in open-water nurseries, capitalizing on herbivory is a simple and costeffective method for increasing nursery production.



Fig. 1. Trends in peer-reviewed literature focused on coral reef restoration. (a) Number of publications from 1991 to 2019 that included some aspect of coral reef restoration categorized by the type of publication. (b) Experimental coral reef restoration publications grouped into the aspect of study undertaken for publications that explicitly addressed coral restoration from 1991 to 2019. An individual publication could be counted towards multiple aspects.

Perhaps the simplest way to incorporate the benefits of herbivory in coral restoration is to conduct restoration within protected areas where herbivore populations are assumed to be larger (Shaver and Silliman, 2017). Indeed, many restoration manuals recommend that projects take place within marine protected areas to capitalize on their existing management and protection status (*e.g.* Edwards, 2010; Johnson et al., 2011a) and many coral restoration projects take place within MPA boundaries. However, in many regions marine protection is absent, or enforcement is weak, and the anticipated benefits of marine protected areas are not tangible (*e.g.* Cox et al., 2017). Furthermore, restoration often needs to occur outside of protected areas, making this an imperfect solution. Simulating herbivory *via* removing algae by hand has occasionally been conducted in some restoration projects (reviewed by Ceccarelli et al., 2018) but is labor intensive and algae return in the absence of adequate top-down pressure (McClanahan et al., 2011).

Alternatively, when protection is not feasible and herbivory rates are low, the enhancement of structural complexity in conjunction with restoration can attract animals, including herbivores, that may benefit outplanted corals (Graham and Nash, 2013; Lee, 2006). For instance, Shantz et al. (2015), found that coral outplants placed near vertical structures where fishes sheltered grew faster and were subject to less algal competition than corals placed at locations where fishes did not shelter. However, degraded reefs lose vertical relief as they erode and this flattening reduces the biomass and diversity of animals present (Alvarez-Filip et al., 2009). Reconstructing lost habitat can facilitate the return of species (Goodsell and Champan, 2009) and is frequently a major goal of coral restoration (Boström-Einarsson et al., 2020). Yet, experimental studies indicate that most corals are outplanted at sizes or densities unlikely to generate beneficial impacts on the local fish community (Huntington et al., 2017; Ladd et al., 2016; Ladd et al., 2019a). Thus, artificial reefs that quickly increase structure and enhance fish densities on degraded reefs (e.g. Thanner et al., 2006) may be useful for jumpstarting trophic interactions. However, deploying artificial structures are can have numerous pitfalls and care must be taken to avoid inadvertently introducing unnatural substrate or habitat that may be detrimental to the developing community (Bulleri and



Fig. 2. Number of publications that included trophic ecology in the context of coral reef restoration. Main plot shows the total number of studies from 1991 to March of 2020. Dark gray shading represents publications that explicitly considered restoration, light gray are studies that did not explicitly consider restoration but have restoration applications. The inset barplot displays the proportion of publications that focused on particular trophic interactions. Some publications included multiple trophic interactions and thus were counted more than once for the inset barplot.

Chapman, 2010; Grossman et al., 1997; Powers et al., 2003). Alternatively, dedicating space and resources to growing a few large coral colonies in nurseries that could be mixed with smaller outplants could provide an alternative to deploying artificial structures and avoid introducing unnatural substrates to degraded reefs.

Finally, stocking restoration sites with herbivores is beginning to garner attention as a feasible strategy. Using theoretical models, Obolski et al. (2016) predicted that restocking degraded reefs with herbivores could be a cost-effective tool to accelerate the recovery of coral populations. Similarly, in manipulative experiments Chiappone et al. (2006) found that patch reefs in the Florida Keys, USA where populations of long-spined sea urchin (Diadema antillarumi) were stocked had less macroalgae and higher coral cover control than reefs that received no urchins. On a larger scale, Hawaii's Division of Aquatic Resources (DAR) combined the manual removal of ~19,000 kg of invasive macroalgae with the release of nearly 100,000 captive bred Tripneustes sea urchins on two reefs to test their efficacy in controlling invasive algae (Neilson et al., 2018). In the Caribbean, long-spined urchins, which were one of the most abundant herbivores on Caribbean reefs until an unknown disease killed over 98% of the population in the 1980's (Lessios et al., 1984; Sammarco, 1982), are a natural candidate for restocking (Maciá et al., 2007). Through advancements in aquaculture long-spined urchins can now be bred in captivity (Sharp et al., 2018) and the relative success of the Hawaiian DAR program suggests that populations could be restored on large scales in conjunction with coral restoration projects. In perhaps the most ambitious example of this joint-restoration strategy to date, the US National Oceanic and Atmospheric Administration is launching an initiative to pair coral outplanting with the local restoration of long-spined urchins and Caribbean king crab (Maguimithrax spinosissimus) at sites throughout the Florida Keys (NOAA, 2020).

3.2. Corallivory

Coral predation (i.e. corallivory) is a chronic source of tissue loss and mortality for many species of coral (Rotjan and Lewis, 2008). Common invertebrate coral predators include sea stars, polychaete worms, and carnivorous snails (Baums et al., 2003; De'ath et al., 2012; Glynn, 1962), all of which can profoundly influence coral populations. For example, before recent consecutive mass bleaching events on Australia's Great Barrier Reef (Hughes et al., 2017, 2018), predation by the corallivorous crown-of-thorns seastar (COTS; Acanthaster planci) was the largest driver of coral mortality on the Great Barrier Reef (De'ath et al., 2012). Fishes, including many butterflyfishes, triggerfishes, pufferfishes, and parrotfishes are also common corallivores (Bonaldo and Rotjan, 2018; Burkepile et al., 2019; Rotjan and Lewis, 2008). These teleost corallivores are typically considered to be less of a threat to corals than major invertebrate corallivores, but in some instances can consume substantial amounts of coral (Cole et al., 2008; Mumby, 2009; Rotjan and Lewis, 2008). Additionally, both teleost and invertebrate corallivores can disrupt coral' microbiomes when they feed (Shaver et al., 2017; Ezzat et al., 2020). For fishes, the impact of these microbial shifts on disease dynamics remains unclear whereas invertebrates like the bearded fireworm (Hermodice carunculata) are known reservoirs for coral diseases (Sussman et al., 2003) and the short coral snail (Coralliophila galea; formerly C. abbreviata) directly transfers diseases among the corals it preys on (Williams and Miller, 2005). Furthermore, corallivory by short coral snails makes their coral prey more susceptible to bleaching (Shaver et al., 2018). Accordingly, minimizing the negative effects of corallivory should be a priority in restoration (Ladd et al., 2018; Shaver and Silliman, 2017).

We identified 17 studies in our literature review that examined corallivory and coral restoration. Eight of these studies explicitly addressed corallivory in the context of coral restoration. Four were reviews or idea pieces that focused broadly on coral restoration and gave varying degrees of attention to corallivory. Two studies examined the effects of grazing on the survival and growth of coral spat (Baria et al., 2010; Linden and Rinkevich, 2017). While both of these studies found that caging enhanced the survival of coral recruits, Baria et al. (2010) attributed the observed increase in mortality of uncaged recruits to incidental removal by grazing fishes. Indeed, parrotfish grazing can be a significant source of recruit mortality (Edmunds et al., 2014; Nozawa, 2008), but these effects are mediated by parrotfish size (Shantz et al., 2020). Therefore, when outplanting or seeding reefs with sexual recruits it may be beneficial to protect the outplants for the first few months using mesh with large enough openings to allow small herbivores access while excluding the largest fishes.

Although the overall benefits of parrotfish herbivory typically outweigh the detrimental effects of periodic corallivory (Bonaldo and Rotjan, 2018; Mumby, 2009), parrotfish corallivory can exact an intense toll on some adult coral species. For instance, the distribution of thin finger coral (Porites divaracata), is limited by intense parrotfish predation (Miller and Hay, 1998). Furthermore, as coral cover declines, corallivory may become concentrated on fewer remaining live corals, amplifying the negative effects of coral predators (Burkepile, 2012; Shantz et al., 2011). This consolidation of coral predation on fewer coral prey is particularly relevant for restoration, where sites in need of coral restoration, by their very nature, have low coral cover. At small scales, research suggests that corals may perform best when outplanted at moderate densities $(3-4 \text{ colonies } m^{-2}; \text{ Goergen and Gilliam, 2018};$ Ladd et al., 2016). However, on reef-wide scales it remains unknown how restoring coral cover impacts the *per capita* rates of corallivory. Thus, research examining how changing coral cover can concentrate or dilute coral predation will be useful to inform restoration strategies.

In contrast to coral eating fishes, studies of corallivorous invertebrates were more common in our Web of Science search. Thirteen studies examined invertebrate corallivory in coral restoration (Supplemental Table 1). On Pacific reefs, the focus was exclusively on COTs, voracious coral predators that are absent in the Atlantic and Caribbean. In the Caribbean region, the most studied corallivores in our literature review were bearded fireworms and short coral snails. All three of these corallivore groups cause substantial coral mortality. For example, in 2005 an outbreak of COTs in Moorea, French Polynesia reduced coral cover along the island's north shore by ~90% (Kayal et al., 2012). Likewise, in the Caribbean major coral mortality occurs both from fireworm and snail predation, as well as increases in coral disease and bleaching susceptibility driven by these predators' feeding (Shaver et al., 2018; Williams and Miller, 2005, 2012).

Minimizing invertebrate coral predation presents a substantial challenge for restoration practitioners. Like corallivorous fishes, the concentration of invertebrate corallivores present on an individual coral can increase as coral density declines (Baums et al., 2003), making density an important consideration for restoration planning. Likewise, Johnston and Miller (2014) found that outplanting Caribbean staghorn coral (Acropora cervicornis) in mixed-species assemblages rather than conspecific stands significantly reduced predation by coral snails. Thus, simple changes in restoration design could have important consequences on the success or failure of coral restoration efforts. However, manual removal and culling remain the most common methods of controlling invertebrate corallivores (e.g. Rivera-Posada et al., 2013; Williams et al., 2014) and projects are even underway to automate this process (e.g. Dayoub et al., 2015). Although labor intensive, manual corallivore removal programs can provide moderate levels of relief (Pratchett et al., 2017 and references within; Williams et al., 2014) but the long larval duration and potential for long-distance dispersal of all three corallivore groups necessitates continuous upkeep (Ahrens et al., 2013; Johnston and Bruckner, 2010; Timmers et al., 2012).

Alternatively, trophic cascades, *i.e.*, "indirect species interactions that originate with predators and spread downward through food webs" (*sensu* Ripple et al., 2016), could present natural, self-sustaining processes that could be exploited to minimize corallivory (Shaver and Silliman, 2017; Fig. 3). For example, white grunts (*Haemulon plumierii*)



Fig. 3. Schematic diagram highlighting how predation by piscivores, invertivores, and invertebrates can help reduce coral mortality, and disease caused by corallivorous invertebrates and damselfishes. Piscivores can provide indirect benefits to corals by praying on damselfish that directly kill corals and increase coral-algal competition by farming algae and chasing away herbivores. Similarly, invertivores such as fish and deltoid rock snails reduce coral predation by corallivorous snails to indirectly benefit corals.

and sand tilefish (Malacanthus plumieri) are two Caribbean fishes that consume bearded fireworms (Ladd and Shantz, 2016). Similarly, giant tritons (Charonia tritonis) feed on COTs on Pacific reefs and deltoid rock snails (Thais deltoidea) are carnivorous gastropods that prey on short coral snails in the Caribbean (Sharp and Delgado, 2015). In one of the only studies to date that has directly tested how predation could be leveraged to facilitate restoration, Delgado and Sharp (2020) found that transplanting nursery-raised colonies of Caribbean staghorn coral in conjunction with deltoid rock snails decreased corallivory and tissue loss in restored corals. Furthermore, the mere presence of rock snails induced escape responses in short coral snails, reducing the amount of time these corallivores spent feeding on transplanted colonies (Delgado and Sharp, 2020). These findings suggest that nonconsumptive effects such as behaviorally-mediated trophic cascades (Schmitz et al., 1997), may be important, yet underappreciated, pathways that restoration can take advantage of to promote the recovery of degraded reefs.

3.3. Damselfishes

Damselfishes warrant special consideration as they can both support or undermine coral restoration (Ladd et al., 2018). While not strictly corallivores, algal-farming damselfishes are a chronic source of tissue mortality when they colonize and kill portions or entire colonies of coral to create algal "gardens" (Potts, 1977; Precht et al., 2010). Colonization by algal-farming damselfish can reduce coral growth rates and is positively correlated with coral diseases (Casey et al., 2015; Vermeij et al., 2015). Additionally, when defending their gardens from other fishes, damselfishes' territorial behavior can reduce beneficial processes like herbivory (White and Donnell, 2010), potentially driving behaviorally-mediated trophic cascades that work against restoration efforts (Catano et al., 2014; Ladd et al., 2019a). On the other hand, damselfishes can also provide benefits to the corals they inhabit. By sheltering within coral branches, damselfishes provide beneficial fishderived nutrients directly to their coral hosts (See Consumer-derived nutrient cycling below). Furthermore, the aggressive behavior of some species will drive off coral-eating fishes (Johnson et al., 2011b) and reduce invertebrate corallivory (Schopmeyer and Lirman, 2015). Thus, when considering the impact of damselfish on coral restoration, it is necessary to take into consideration the context of damselfish trophic interactions at specific restoration sites.

In our literature review, negative effects of damselfishes were overwhelmingly associated with Caribbean restoration efforts, likely because Caribbean staghorn coral, the primary species used for restoration in the region (Schopmeyer and Lirman, 2015), is the preferred habitat for algal-farming damselfishes (Precht et al., 2010). Accordingly, due to the paucity of staghorn corals in the Western Atlantic and Caribbean, outplanted colonies are often quickly colonized by damselfishes (e.g. Goergen et al., 2019). In such situations, reducing coral colonization by damselfishes could improve restoration outcomes (Ladd et al., 2018). Once again, trophic cascades may play a central role in reducing these adverse effects (Fig. 3). For instance, on reefs across Curacao, Vermeij et al. (2015) found an inverse relationship between piscivore biomass and damselfish abundance, likely due to both direct and indirect effects of predators. Furthermore, areas with less damselfish were also characterized as having a lower prevalence of coral disease (Vermeij et al., 2015). Thus, restoration practitioners could couple outplanting corals with fishing restrictions or do so within successful marine protected areas with intact piscivore populations to reduce the prevalence or intensity of damselfish-induced coral mortality. Alternatively, augmenting the structural complexity at outplanting sites can attract predators just as it does herbivores (Graham and Nash, 2013; Lee, 2006) and may provide a means of limiting the negative impacts of algal-farming damselfishes.

Factors regulating damselfish populations likely vary widely among reefs, making it unlikely that the already difficult task of protecting higher trophic levels alone could be a viable solution in some locations. Across the Caribbean, Precht et al. (2010) found no relationship between fishing pressure and damselfish abundance and suggested that microhabitat availability was the major driver of damselfish distribution. Moving forward, studies that evaluate how factors like predator biomass or coral abundance affect damselfish dynamics and subsequent restoration success would provide valuable insights to improve coral reef restoration approaches.

4. Coral heterotrophy

Although reef-building corals depend on photosynthetically-derived nutrients from their endosymbiotic algae for survival, corals also possess varying degrees of heterotrophic capability to supplement their nutrition (Ferrier-Pagès et al., 2010; Grottoli et al., 2006; Porter, 1976). Corals actively consume zooplankton, phytoplankton, and particulate and dissolved organic matter (Houlbrèque and Ferrier-Pagès, 2009). Feedings rates are influenced by prey availability and water motion, but coral morphology ultimately dictates the types and sizes of prey consumed by different coral species (Palardy et al., 2005; Sebens et al., 1998, 1997; Seemann et al., 2013). Different species also demonstrate substantial species-specific plasticity in feeding rates in response to their metabolic demands. For instance, under low light availability the lesser star coral (Goniastrea retiformis) more than doubles its feeding rate to compensate for declines in photosynthesis. In contrast, hump coral (Porites cylindrica) has limited heterotrophic capacity and can only marginally increase feeding rates when light levels decline (Anthony and Fabricius, 2000). As a result, heterotrophy is highly variable between species but typically provides 15-35% of the metabolic reguirements of healthy coral colonies (Houlbrèque and Ferrier-Pagès, 2009).

Increasing rates of coral heterotrophy often directly translates to improved physiological performance of the holobiont (Houlbrèque and Ferrier-Pagès, 2009). The energy and nutrients corals obtain from feeding can increase photosynthesis, protein synthesis, and lipid reserves, which in turn can be utilized to enhance growth, calcification, and resistance to environmental stressors (Borell et al., 2008; Levy et al., 2016; Tremblay et al., 2016). For example, tissue growth in hood corals (Stylophora pistillata) fed zooplankton was 2 to 8-fold greater than growth in unfed colonies and calcification rates were ~ 30% higher (Ferrier-Pagès et al., 2003). Similarly, when corals' endosymbionts are lost during bleaching events, species with greater heterotrophic capacity have larger energy reserves to prolong their survival and can increase their feeding effort to meet their energetic requirements until symbiosis is reestablished (Grottoli et al., 2014, 2006; Hughes and Grottoli, 2013). Logically, it follows that the improved physiological performance and stress resistance that corals obtain from feeding could be harnessed to benefit restoration efforts.

Surprisingly, despite the widely reported importance of coral heterotrophy there were only eight published experiments in our literature review that explored heterotrophy in a restoration context (Supplemental Table 1). Six of these studies focused on supplemental feeding as a means of increasing the growth and survival of propagated coral fragments. These studies used a variety of coral species and diets but showed that supplemental feeding increased coral growth in the majority of instances (Fig. 4). Optimal diets are likely to differ between species and growth in seven of the eight coral species tested increased under at least one diet, suggesting that instances where feeding did not benefit corals were most likely a result of offering incompatible foods. Artemia nauplii were the most commonly used food and benefited four of the five coral species tested. These easily hatched zooplankton have been suggested to be the most economic option for supplemental feeding (Osinga et al., 2012; Petersen et al., 2008) but can still add substantial costs in labor and time. However, when factoring in differences in growth and survival between fed and unfed colonies, feeding may yield substantially more coral production in ex situ nurseries for similar costs (Toh et al., 2014).

Beneficial effects of coral heterotrophy were observed in both adult colonies and recently metamorphosed recruits raised in *ex situ* nurseries. Seeding degraded reefs with sexual recruits is a promising way of cheaply restoring coral cover and genetic diversity (Baums et al., 2019). However, a major obstacle for this form of restoration has been the low probability of recruit survival (Chamberland et al., 2017; Guest et al., 2014). The improved growth and physiological condition of fed, nursery reared recruits could therefore provide potentially

substantial improvements in the use of sexual recruits in coral restoration (Toh et al., 2014). Supplemental feeding also increased the lipid reserves and ability of two nursery raised species to survive a simulated thermal stress event (Tagliafico et al., 2017), suggesting that feeding corals in nurseries could "prime" colonies prior to outplanting to increase survival, particularly during warm summer months when stress and energetic demands may be highest. Taken as a whole, this work provides compelling evidence that supplemental feeding can enhance *ex situ* coral production and outplanting success.

Whether supplemental feeding can be scaled up to benefit *in situ* nurseries or is even beneficial for in-water nurseries is unclear. In aquaria at *ex situ* nurseries food may easily become limiting whereas resource depletion is less likely to occur in the ocean. Indeed, supplemental feeding provided no benefits for the Pacific staghorn coral *A. millepora* maintained in unfiltered, flow-through seawater, suggesting that the benefits of feeding corals in *ex situ* nurseries may simply result from preventing resource depletion (Conlan et al., 2018). Still, when corals are kept at high densities in nurseries it could cause localized resource depletion (Sebens et al., 1997; Fabricius and Metzner, 2004) and the variable heterotrophic capacity of many species suggests that at least some are likely to benefit from supplemental feeding (Anthony and Fabricius, 2000; Grottoli et al., 2006).

The logistics of scaling up feeding operations for in situ nurseries presents another challenge. In ex situ nurseries, corals are maintained in a relatively small volume of water and the environment can be carefully controlled. In contrast, in situ nurseries lack this control and large amounts of supplemental foods are likely to be lost without reaching the target corals. One plausible solution could be constructing inwater nurseries in productive locations where food is abundant. For instance, linking coral nurseries to aquaculture sites such as fish farms, which can generate considerable amounts of pollution from uneaten feed and excreted waste (Serpa and Duarte, 2008) could provide an excellent opportunity for integrated multi-trophic aquaculture (Bongiorni et al., 2003a, 2003b). However, these locations may also be linked to increased risks associated with eutrophication, such as smothering, algal overgrowth, and coral diseases (Fabricius, 2005; Vega Thurber et al., 2014; Zaneveld et al., 2016) and may not be appropriate for many coral species.

Ultimately, taking advantage of the heterotrophic capacity of corals can not only improve the condition of nursery reared corals but can benefit corals in the field. Fed corals grow faster and are more likely to survive environmental stress than their unfed counterparts. Therefore, outplanting species with broad diets that feed frequently to locations with an abundant food supply could increase coral cover and habitat creation faster than planting species that are unable to increase their feeding. Additionally, animals with a higher capacity for obtaining energy via heterotrophy may be more likely to survive inevitable bleaching events than their less heterotrophic counterparts (Grottoli et al., 2006; Rodrigues and Grottoli, 2007). Consequently, restoring populations of corals capable of high rates of heterotrophic feeding could benefit restoration efforts by both generating reefs more resilient to climate change, and more quickly providing desirable ecosystem services. Given the potential benefits, research specifically addressing incorporating heterotrophy into restoration warrants urgent attention. For example, important knowledge gaps in this area include (1) resolving the degree of heterotrophic capacity of different species and their suitability to achieve restoration outcomes, (2) determining optimal diets for different species that are commonly used in restoration, and (3) the feasibility, risks, costs, and benefits, of scaling up feeding programs to benefit in situ nurseries.

5. Consumer-derived nutrient cycling

Over the past decade, there has been mounting evidence that consumer-derived nutrient cycling plays a critical role in structuring reefs (Allgeier et al., 2014; Allgeier et al., 2020; Burkepile et al., 2013;



Fig. 4. The effect size of supplemental feeding with different diets on different species of coral from our literature review. Effect sizes were calculated as Hedge's g, or the average Hedge's g when the same species of coral was provided with the same diet in multiple experiments.

Layman et al., 2011; Benkwitt et al., 2019). On un-fished reefs, nutrient delivery and recycling from fishes can be orders of magnitude higher than other processes and constitute a critical source of nutrients for corals (Burkepile et al., 2013). For example, corals utilize the inorganic ammonium and phosphorus excreted by fishes to fuel photosynthesis (Shantz and Burkepile, 2014). In turn, corals supplemented with fish-derived nutrients have faster growth and calcification rates, and greater carbohydrate, lipid, and protein reserves (Ezzat et al., 2015; Holbrook et al., 2008; Meyer and Schultz, 1985). However, as coral cover declines, a greater percentage of consumer-derived nutrients are taken up by algae, fueling algal growth and potentially reinforcing phase-shifts to algae dominated reefs (Burkepile et al., 2013). Given the potential for consumer-derived nutrients to benefit corals and strengthen environmental feedback, these subsidies could directly and indirectly enhance restoration success.

Currently, very few studies have considered the role that consumerderived nutrient cycling plays in coral restoration programs. In their perspective piece, Shaver and Silliman (2017) note that nutrient subsidies, including fish-derived nutrients, are likely important for coral productivity, while (Ladd et al., 2018) recommend leveraging fish aggregation sites as recovery nodes within degraded reefs. However, empirical evidence that consumer-derived nutrients can benefit coral restoration remains limited. Only two studies in our literature review experimentally assessed the impact of consumer-derived nutrients in a restoration context (Huntington et al., 2017; Shantz et al., 2015). Promisingly, both suggest that the growth rates and physiological condition of Caribbean staghorn transplanted to locations with high fish biomass is greater than at locations with low biomass. Of note, both studies also showed increased nutrient content in the tissue of macroalgae growing at locations with high fish biomass. The potential for fish-derived nutrients to fuel both coral and algae growth supports the hypothesis that these subsidies could reinforce coral- or algaedominated states on reefs and can inform restoration strategies (Burkepile et al., 2013). For instance, on sites with low structural complexity where fishes are widely dispersed, outplanting efforts may need to be focused to achieve sufficient coral density or structural complexity to aggregate fishes around outplants and shift the benefits of fish-derived nutrients from algae to corals. Indeed, surveys across Florida and the Caribbean found that positive relationships between fish and coral density only occurred in the densest staghorn thickets (Huntington et al., 2017). Furthermore, restoration efforts that successfully aggregate fishes around outplants will not only improve coral growth via delivery of fish-derived nutrients but could create a heterogeneous nutrient landscape that concentrates grazing on higher quality forage at enriched sites (Shantz et al., 2017, 2015). Thus, finding ways to facilitate the heterogenous delivery of fish-derived nutrients can help create nutrient hotspots that are amenable to restoration.

5.1. Benthic-pelagic coupling

An abundant supply of exogenous plankton represents a potentially important, yet underappreciated, driver of multiple trophic cascades that could benefit restoration efforts on coral reefs (Hamner et al., 2007; Morais and Bellwood, 2019; Polunin, 1996; Fig. 5). Planktivorous fishes constitute more than 20% of reef fish species and are a substantial component of total fish biomass on many reefs (Bellwood and Hughes, 2001; Sandin et al., 2008). Planktivores are the primary importers of nutrients from pelagic sources, effectively coupling benthic and pelagic areas (Hamner et al., 1988). This benthic-pelagic coupling drives up to 40% of fish productivity at some reef sites (Morais and Bellwood, 2019) and provides a food source for higher trophic levels (Hamner et al., 2007).

Beyond direct benefits from increased food supply for fishes (Hamner et al., 2007; Polunin, 1996) and corals (Houlbrèque and Ferrier-Pagès, 2009), increased benthic-pelagic coupling could confer a suite of indirect benefits to coral reef restoration efforts. For instance, the nutrients excreted and egested by planktivorous fishes can increase the growth rates of the corals they shelter within (Holbrook et al., 2008; Meyer and Schultz, 1983), in turn fueling positive feedbacks by creating additional structure to house larger fish populations. Increased refuge



Fig. 5. Conceptual diagram illustrating how benthic-pelagic coupling can be leveraged to advance multiple aspects of coral reef restoration.

space provided by larger branching coral colonies can also increase habitat available for colonization by mutualistic invertebrates, such as guard crabs from the genus *Trapezia*, which benefit corals by removing sediments (Stewart et al., 2006) and likely *via* additional nutrient cycling. These mutualists also protect their host colonies from coral predators (McKeon et al., 2012; McKeon and Moore, 2014), and thus could help corals survive biological perturbations. Incorporating pathways that take advantage of pelagic inputs that can promote these positive interactions would further advance our ability to effectively restore degraded reefs (Fig. 5).

6. Conclusions and future directions

Trophic ecology has improved our understanding of productivity, community structure, and resilience on tropical coral reefs (Estes et al., 2011; Muscatine et al., 1989; Odum and Odum, 1955; Randall, 1965). Now, as the need for strategies to maintain and restore rapidly degrading reefs becomes increasingly urgent, it is important that we take advantage of the accumulated knowledge from the past halfcentury to facilitate coral restoration. Promisingly, researchers and restoration practitioners are rising to the challenge, as evidenced by the rapidly increasing number of publications in our literature review and the shift from methodological towards ecological approaches (Fig. 1). Although our focus here is restricted to the patterns and insights that can be gleaned from peer reviewed publications, it is important to recognize that a large portion of restoration is conducted by organizations and agencies that lack the incentive or resources to publish their findings (Boström-Einarsson et al., 2020). Thus, there are likely case studies from projects that have included trophic interactions which remain unpublished. Because the most widely used restoration guidelines are drawn from published research (e.g. Edwards, 2010; Johnson et al., 2011a), data from these unpublished projects are a valuable resource and missed opportunity to advance the field of coral reef restoration. Therefore, researchers and restoration practitioners should continue to strive to build collaborations and share data to help disseminate the outcomes of successful and unsuccessful restoration projects to a broader audience.

Processes such as herbivory, predation (including corallivory), coral heterotrophy, and consumer-derived nutrient cycling are being recognized as potentially important tools that can be harnessed and manipulated to improve coral restoration outcomes. However, these are by no means the only important trophic interactions on tropical reefs that warrant consideration. For example, sponges are increasingly dominant members of contemporary reef communities that frequently overgrow and outcompete corals (Ladd et al., 2019b; Lesser and Slattery, 2020). Thus, strategies to protect or increase sponge predators at restoration sites may help corals resist competitive exclusion by sponges (Loh et al., 2015). Top-down mediation of spatial competition to favor corals is just one example of how expanding our thinking to utilize natural processes could make restoration more effective and affordable.

While trophic ecology can offer improvements and solutions to problems that hamper coral restoration, it is important to recognize that tropical reefs and the conditions they exist under are fundamentally changing. In these new and evolving coupled human-natural systems, processes that were once paramount for shaping communities may have little bearing on some reefs today (Gilman et al., 2010; Urban et al., 2012). For example, well-regulated no-take marine reserves can effectively restore animal biomass, diversity, and many trophic interactions on tropical reefs (Sala and Giakoumi, 2018) but they cannot guarantee the return to previous ecological states (Toth et al., 2014). Accordingly, while well studied ecological principles can provide guidance for restoration practitioners, it is important that restoration projects be considered in their own unique context and the utility of specific trophic interactions determined on a case by case basis.

Thus, empirically testing methods of incorporating trophic interactions in restoration designs to assess their costs, effectiveness, and utility under different scenarios is an important priority. For example, while herbivory undoubtedly benefits corals (Burkepile and Hay, 2006), NOAA predicts that restocking long-spined urchins and Caribbean king crab at seven restoration sites in the Florida Keys will cost approximately \$7,000,000 USD (NOAA, 2020). Projects like this provide excellent opportunities to assess how novel interventions impact restoration outcomes and compare these strategies with traditional outplanting or remediation strategies like improving water quality. Doing so will help identify the most effective approaches to restoring degraded reefs. Ultimately, however, both remediation of the underlying drivers of coral reef decline, including CO₂ emissions, and active replenishment of coral populations will be needed to realize long-term restoration success on tropical reefs. Supplementary data to this article can be found online at https://doi. org/10.1016/j.fooweb.2020.e00149.

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Erratum regarding missing Declaration of Competing Interest statements in previously published articles

Declaration of Competing Interest statements were not included in the published version of the following articles that appeared in previous issues of *Food Webs*.

The appropriate Declaration/Competing Interest statements, provided by the Authors, are included below.

 "If you build it, they will come: Restoration positively influences free-living and parasite diversity in a restored tidal marsh" [Food Webs, 2020; 25:e00167] https://doi.org/10.1016/j.fooweb.2020. e00167

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- "Biofuel management has limited effects on forest nutrients and avian resource assimilation" [Food Webs, 2019; 22:e00135] https://doi.org/10.1016/j.fooweb.2019.e00135

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 "Eutrophication disrupts summer trophic links in an estuarine microbial food web" [Food Webs, 2019; 20:e00121] https://doi.org/ 10.1016/j.fooweb.2019.e00121 Declaration of competing interest: The Authors have no interests to declare.

- 6. "A review of species role concepts in food webs" [Food Webs, 2018; 16:e00093] https://doi.org/10.1016/j.fooweb.2018.e00093 Declaration of competing interest: The Authors have no interests to declare.
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