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Interactions between coral restoration and fish assemblages: implications for reef management

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Abstract

Corals create complex reef structures that provide both habitat and food for many fish species. Because of numerous natural and anthropogenic threats, many coral reefs are currently being degraded, endangering the fish assemblages they support. Coral reef restoration, an active ecological management tool, may help reverse some of the current trends in reef degradation through the transplantation of stony corals. Although restoration techniques have been extensively reviewed in relation to coral survival, our understanding of the effects of adding live coral cover and complexity on fishes is in its infancy with a lack of scientifically validated research. This study reviews the limited data on reef restoration and fish assemblages, and complements this with the more extensive understanding of complex interactions between natural reefs and fishes and how this might inform restoration efforts. It also discusses which key fish species or functional groups may promote, facilitate or inhibit restoration efforts and, in turn, how restoration efforts can be optimised to enhance coral fish assemblages. By highlighting critical knowledge gaps in relation to fishes and restoration interactions, the study aims to stimulate research into the role of reef fishes in restoration projects. A greater understanding of the functional roles of reef fishes would also help inform whether restoration projects can return fish assemblages to their natural compositions or whether alternative species compositions develop, and over what timeframe. Although alleviation of local and global reef stressors remains a priority, reef restoration is an important tool; an increased understanding of the interactions between replanted corals and the fishes they support is critical for ensuring its success for people and nature.

KEYWORDS

corallivores, cryptics, damselfishes, herbivores, nutrients, predators, restoration, shade

1 | INTRODUCTION

Coral reefs provide critical ecosystem services, including fisheries, coastal protection and tourist income, to millions of people (Barbier, 2017; De Groot *et al*., 2012; Woodhead *et al*., 2019). Despite their global importance, protection is currently inadequate (Mora *et al*., 2006; Pressey *et al*., 2015; Cox *et al*., 2017), and consequently key indicators of reef health, such as coral cover, are declining (Bruno & Selig, 2007; Gardner *et al*., 2003; Hughes *et al*., 2017; Pandolfi *et al*., 2003). This reef degradation is driven by anthropogenic impacts, including overfishing, global climate change, coral disease, sedimentation, extensive coastal development, introduction of invasive species and the release of pollutants (Hoegh-Guldberg *et al*., 2017; Hughes *et al*., 2003). The loss of coral cover and complexity caused by these stressors is affecting the ecosystem services provided by reefs (Cesar *et al*., 2003; Pratchett *et al*., 2014). Global threats require international action, but managing local threats is also critical (Kennedy *et al*., 2013). Although establishing marine reserves is perhaps the most commonly used technique to address local reef degradation, it has been suggested that a wider range of methods are required to manage tropical coastal resources and to maintain reef processes (Allison *et al*., 1998; Anthony *et al*., 2015; Aswani *et al*., 2015; Rogers *et al*., 2014). Reef restoration is one of these potential tools to augment other management methods (Lirman & Schopmeyer, 2016).

The terms reef "restoration" and "rehabilitation" are often used interchangeably in the coral reef literature. Restoration is generally defined as bringing a degraded ecosystem back as close as possible to its original natural state, whereas rehabilitation refers to situations where the functional and structural properties of an ecosystem are replaced, not necessarily in the same manner as the original state (Edwards & Gomez, 2007). In most cases it is likely that although restoration may be desired, rehabilitation is the most achievable outcome, and a shift in management goals from a return to original species composition to the need to maintain ecological functions and ecosystem services of reefs has been suggested (Graham *et al*., 2014; Hughes *et al*., 2017). Effort may not always be focused on restoring original reefs, but sometimes creating new habitat for reef communities. There are many examples of entirely artificial reefs (*e.g*., "reef balls" or sunken ships), where the main focus is on the deployment of artificial structures, usually in areas where reefs did not previously exist or where they have been entirely degraded away, which can then be colonised by marine organisms (Baine, 2001). Although the authors draw on some of the artificial reef literature, the main focus of this review is specifically on how the restoration of existing coral reefs benefits, and is benefitted by, fishes, while acknowledging the potential addition of artificial structures being deployed as part of the process.

The most widespread method of coral reef restoration involves the introduction and distribution of nursery-reared or wild-collected coral fragments in areas previously affected by human actions or adverse environmental conditions (Johnson *et al*., 2011; McLeod *et al*., 2019a; Precht, 2006). Coral fragments are either directly transplanted to the substrate (Forrester *et al*., 2012; Ladd *et al*., 2019; Lohr *et al*., 2017) or may be attached to artificial structures which have proven successful in environments dominated by mobile substrata such as coral rubble (Clark & Edwards, 1999; Fadli *et al*., 2012; Williams *et al*., 2019). By outplanting corals, managers aim to enhance ecological processes and re-create self-sustaining naturally growing habitats due to the ability of corals to colonise and build complex structures (Edwards, 2010; Edwards & Gomez, 2007). In some instances, other techniques may be used such as the culture and release of coral larvae or juveniles (Chamberland *et al*., 2017; dela Cruz & Harrison, 2017; Heyward *et al*., 2002), the transplantation of entire mature coral colonies (Mbije *et al*., 2013; McLeod *et al*., 2019b; Schopmeyer & Lirman, 2015) or other organisms such as giant clams (Cabaitan *et al*., 2008), coral gardening including an intermediate coral nursery phase (Bongiorni *et al*., 2011; Frias-Torres *et al*., 2015; Horoszowski-Fridman *et al*., 2015), algal removal (McClanahan *et al*., 1999, 2000, 2001) or even the deployment of artificial structures alone to provide a stable substrate for future colonisation (Jayanthi *et al*., 2020; Ng *et al*., 2017; Thanner *et al*., 2006). A description of these coral reef restoration methods can be found in Boström-Einarsson *et al*. (2020), forming the basis for examining the relationship between these techniques and fish assemblages in this review.

Although restored reefs remain susceptible to global influences such as climate change, disease and pollution, reef restoration may be the last resort for immediate reinforcement of critical ecological functions and services for reefs that have degraded significantly and may not have sufficient resilience to recover (Rinkevich, 2008), or where there is a desire to speed up recovery. For example, there is evidence that reef restoration methods can be used to manage tropical reefs damaged by destructive fishing practices (Fox *et al*., 2005; Raymundo *et al*., 2007); when sites have been degraded to the state of rubble fields, there is usually little chance for natural recovery without human intervention (Fox *et al*., 2003). This loss of benthic structure can have devastating consequences not only on natural fish populations but also on the livelihoods of coastal communities. Millions of people, mainly in developing countries, are dependent on tropical fisheries for income and protein needs (Cinner *et al*., 2009). Managing reefs through the implementation of restoration projects may help protect and enhance those ecosystem services for the benefit of coastal people (Mumby & Steneck, 2008; Rogers *et al*., 2015).

It is clear that reefs provide multiple benefits for fishes, the main ones being the provision of food, habitat and settlement substrate (Graham & Nash, 2013; Gratwicke & Speight, 2005; Luckhurst & Luckhurst, 1978). For example, some reef-associated fishes rely specifically on live coral, and many more species benefit from structural complexity provided by the reef environment (Coker *et al*., 2014). Consequently, fishes are likely to benefit from restoration, and this is often an implicit or explicit reason for restoring habitat. The importance of fishes in benthic dynamics is also well documented, particularly herbivorous species aiding coral growth and survival by controlling macroalgal cover (Bellwood *et al*., 2004; Hughes *et al*., 2007; Mumby *et al*., 2006a). Nonetheless, although the importance of the interactions between reef fishes and their habitat is well established, reef restoration research has focused almost exclusively on coral

survival (Lirman & Schopmeyer, 2016; Young *et al*., 2012) with research into the effects of adding live coral cover and complexity on fishes in its infancy. This review has identified studies which have monitored effects of coral reef restoration on fishes and *vice versa*. Following searches conducted with the keywords listed in Table S1 and excluding studies where the main aims did not concentrate on restoring coral reef ecosystems, 38 publications are summarised in Table 1. Although a few of these restoration publications have assessed fish populations directly, fishes were more commonly investigated as secondary qualitative observations. Throughout this review the authors consider the bidirectional interactions between fishes and restored reefs (Figure 1), and how this is governed by coral cover and reef complexity and the various functions of fishes on restored reefs. Furthermore, key research questions to help inform coral reef restoration are identified as restoration programmes intensify globally.

2 | THE ROLE OF HABITAT AND SEASCAPE COMPLEXITY

There is a general consensus that the availability of complex coral reef habitat is a prerequisite to abundant and diverse coral reef fish assemblages (Luckhurst & Luckhurst, 1978; Bell & Galzin, 1984; Gratwicke & Speight, 2005; Graham & Nash, 2013). Many reef fishes are dependent on complex corals for habitat, shelter from predators and water movement, foraging, spawning and nesting (Almany, 2004a; Caley & St John, 1996; Johansen *et al*., 2008; Robertson & Sheldon, 1979). Consequently, the global decline of live corals and associated decrease in reef rugosity has affected resident fish populations, and coral reef fisheries (Alvarez-Filip *et al*., 2009; Jones *et al*., 2004; Pratchett *et al*., 2014; Sano *et al*., 1984). Restoration may increase coral cover and habitat complexity on a reef within a relatively short time period with the use of fast-growing coral species, which otherwise would take decades to re-establish naturally (Williams *et al*., 2019). For instance, the reported median length of restoration projects is 12 months, suggesting that coral reef restoration may have rapid effects on coral ecosystems (Boström-Einarsson *et al*., 2020). Nonetheless, although active management methods such as reef restoration have the potential to increase coral cover and fish stocks more quickly compared to some other management tools (Rinkevich, 2005, 2008), reported recovery time frames currently vary from months to decades and appear to be context-dependent (Table 1).

Coral reef restoration can provide shelter for fishes either between coral fragments and/or under constructed structures to which the coral fragments are attached (Clark & Edwards, 1999; Fadli *et al*., 2012). Provision of shelter allows reef fishes to avoid predation (Shulman, 1985), and shelter for herbivorous fishes may in turn help control algal overgrowth on restoration structures, as fish presence has been linked to reduced cleaning maintenance on introduced structures such as coral nurseries (Frias-Torres *et al*., 2015; Frias-Torres & van de Geer, 2015; see the section "The Role of Herbivorous Fishes"). In one of the few studies that have quantitatively investigated the effects of coral transplantation on fish colonisation, populations were surveyed at selected treatment and non-restored degraded control plots prior to transplantation of staghorn coral *Acropora cervicornis* fragments, and then again following restoration (Opel *et al*., 2017). Fish numbers and diversity were significantly greater in restored plots when compared to control plots within a week of the transplantation, demonstrating the fast rate of fish recolonisation, with the benthic structure as the main predictor of change. By the end of the study, experimental sites had no resemblance to one another with regard to fish assemblages present, as each experimental site attracted unique and distinct populations. Therefore, although initial assemblages on restored reefs may reflect recruitment from adjacent reefs and original fish communities, restored sites may also attract new species and create novel fish assemblages. There is, however, mixed evidence that the artificial addition of live coral cover impacts coral fish populations. Whereas other studies have reported increases in fish densities and species richness due to coral transplantation (Cabaitan *et al*., 2008; Clark & Edwards, 1999; Hudson *et al*., 1989; Lecchini, 2003; Yap, 2009), a recent study by Ladd *et al*. (2019) investigating established restoration sites of varying coral transplant densities and maturity revealed little impact of the interventions on fish communities, with the exception of coral-associated damselfishes. As quantitative studies of the effect of coral restoration on fish assemblages are still scarce, with fishes rarely the main focus of restoration publications (Table 1), further research is clearly needed.

Different restoration strategies and designs can influence important ecological processes on reefs. For example, in a patch reef study where low complexity and high complexity corals were transplanted, resident reef predators chocolate grouper (*Cephalopholis boenak*) (Bloch 1790) and brown dottyback (*Pseudochromis fuscus*) Müller & Troschel 1849 had more successful strikes, with prey mortality increasing when low complexity corals were transplanted (Beukers & Jones, 1998). Transplantation of high complexity corals provided greater refuge opportunity for the focal prey fish, juvenile lemon damsel (*Pomacentrus moluccensis*) Bleeker 1853. Nonetheless, the increased complexity associated with restoration may still be beneficial to predatory fishes in the longer term. If prey fishes survive capture by escaping into reef refuges, this enhances reef fish productivity, which in turn increases prey fish numbers (Rogers *et al*., 2014). As prey fish populations rise, some individuals are excluded from refuges through competition, thus exposing them to predators (Holbrook & Schmitt, 2002). The impact of habitat complexity on predators will also vary greatly depending on predatory strategies. Ambush predators may profit from increased structure compared to roaming predators (Almany, 2004b; Rogers *et al*., 2018). Restoration projects may provide prey shelters as well as predation opportunities by promoting complexity at different spatial scales. For example, creating different-sized holes within artificial reefs may benefit both prey and predators (Bohnsack, 1991). Future research should examine how changes in multi-scale coral complexity associated with coral transplantations affect predator–prey interactions (Table 2), and include both consumptive and non-consumptive ("fear") effects (Mitchell & Harborne, 2020).

Although artificial reefs can be different from reefs restored through transplantation, comparisons are still insightful when habitat

TABLE 1 Length of study represents time elapsed since first restoration intervention (*i.e.*, installation of coral nurseries) as well as the timeframe described for censuses of fish assemblages if reported (*in italics*). Summary of existing peer-reviewed publications of coral reef restoration and their impact on fish assemblages as well as studies where fish species have been documented to impact restoration success (*)

Reference	Location	Scale of restoration (m^2)	Length of study (months)	Description of coral restoration methods	Results relating to fish assemblages
Hudson *et al*., 1989	Biscayne, U.S.A.	40	144	Deployment of artificial patch reef of hollow concrete domes. Hard and soft corals were cemented to surface.	10 years post-deployment, fish abundance and richness were higher than unrestored sea floor but lower than natural patch reef.
Bowden-Kerby, 1997	Pohnpei, Micronesia and Puerto Rico	Not reported	36 (*4*)	*Acropora* fragments and cultured whole colonies translocated onto reef flat rubble and sandy back reef.	Qualitative observations of small wrasses feeding on algae growing on dead tissue of coral fragments hours after transplantation promoting coral re-growth. Fish recruitment was higher on whole coral colonies transplanted >20 m compared to <2 m from natural reefs.
Clark & Edwards, 1999	Galu Falhu, Malé, Maldives	600	42 (*42*)	Four types of structures deployed: (a) hollow concrete blocks, (b) Armorflex flexible concrete mattresses, (c) Armorflex onto which corals from nearby reefs were transplanted, (d) rubble-stabilising chain-link fencing.	Hollow blocks and the Armorflex with coral structures attracted the most fish due to higher topographic complexity; all structures were rapidly colonised. Within 1 year, the three structures with higher complexity were supporting fish communities similar in richness and higher in density than undisturbed control reefs. Species composition was significantly different to undisturbed reefs mostly due to higher abundance of *Apogon* spp.
Salvat *et al*., 2002	Bora Bora, French Polynesia	3500	32	Artificial concrete structures with cemented coral colonies deployed on a sandy shallow reef flat.	Qualitative observations of colonisation by a variety of resident and transient reef fishes across nine families which mirrored nearby natural reefs.
Lecchini, 2003	Moorea Island, French Polynesia	400	24 (*24*)	Concrete modules covered with live coral colonies deployed on a sand channel.	Fish abundance increased continuously 2 years post-deployment. Species richness increased during the first 6 months then stabilised. Species composition was significantly different pre-deployment *vs*. 6 months-post deployment. Herbivores, omnivores or small carnivores interacted with the modules while planktivorous juveniles associated with the attached coral colonies. Large transient fishes did not interact with the modules.
Fox *et al*., 2005	Komodo National Park, Indonesia	6430	60 (*1*)	Large-scale substrate stabilisation across four designs: (a) complete coverage with rocks, (b) rock piles spaced every 2–3 m, (c) spur and groove design parallel to water current and (d) spur and groove perpendicular to current.	Qualitative observations of increased fish abundance and diversity at the stabilised plots when compared to unrestored rubble. Several fish families used the deployed rocks as refuge (Serranidae, Anthiinae, Pomacentridae, Acanthuridae, Scaridae, Scorpaenidae, Caesionidae, Zanclidae).
*Quinn & Kojis, 2006	Discovery Bay, Jamaica	Not reported	55	Fragments of wild *Acropora* corals were collected and attached to three types of artificial structures: (a) plastic-coated wire-mesh A-frames, (b) cement disks secured to a wire mesh sheet, (c) suspended nylon lines.	Qualitative observations: *Stegastes* predation on coral transplants secured to A-frames placed on rock or rubble led to high coral mortality. Small-sized wire mesh particularly attracted farming damselfish. Placing A-frames on sand near reefs and using large size wire mesh inhibited algal lawn creation. Placing frames too far away from reefs increased algal growth due to a lack of herbivore grazing. Coral transplants attached to other structures did not display signs of *Stegastes* bites.
*Shafir *et al*., 2006	Gulf of Eilat, Israel	100	10	Coral mariculture success was investigated at a mid-water floating coral nursery installed near a fish farm. Various size coral fragments were glued to plastic pins and placed on plastic frames, themselves secured on a rope net.	Increased nutrients from the fish farm enhanced coral survival and growth: 147–163 fold increase in coral ecological volume and 6-fold increase in height after 306 days. Qualitative observations of algal and fouling removal by resident schools of fishes, in particular *Siganus rivulatus*. Densely packed corals excluded grazers, whereas wider-spaced coral pins led to more intensive grazing. Coral fragments did not experience predation by corallivorous fish.

TABLE 1 (Continued)

Reference	Location	Scale of restoration (m^2)	Length of study (months)	Description of coral restoration methods	Results relating to fish assemblages
Thanner *et al.*, 2006	Bal Harbour, Florida, U.S.A.	15,000	67 (*60*)	Evaluation of the effectiveness of limerock boulders surrounded by an array of prefabricated concrete modules as artificial reef materials.	Fish assemblages differed between the two artificial reef materials and between artificial and natural reefs. Species richness was lower on the artificial reef (boulders and modules) than on natural reefs; nonetheless, resident fish density was highest at the boulder site due to schools of juvenile *Coryphopterus personatus*. Modules saw a gradual decline in species richness over time. Gobiidae and Haemulidae species were most abundant on artificial reefs.
Raymundo *et al.*, 2007	Calagcalag marine protected area, Philippines	87.5	37 (*41*)	Five treatment plots in a rubble field, stabilised with plastic mesh carpets and rock piles.	Rubble areas and initial age rehabilitation areas were characterised by high labrid density. Intermediate age rehabilitation areas were characterised by high labrid and pomacentrid and moderate scarid densities. Healthy reef and older rehabilitation areas were characterised by high pomacentrid, low labrid and moderate scarid densities. Fish biomass increased significantly over time at rehabilitation plots. Herbivores doubled in biomass, with a large but variable increase in biomass of planktivores. Piscivore biomass increased slightly.
Cabaitan *et al.*, 2008	Caniogan Marine Sanctuary, Anda Island, Philippines	25	11 (*14*)	Five treatments: (a) coral transplantation on concrete blocks, (b) giant clam restocking, (c) clam restocking, with coral fragments attached to their shells, (d) deployment of clam shells and (e) controls.	Species richness rapidly increased on the coral, clam+coral and clam treatments (3.5/3.3/3-fold) as opposed to the shell and control treatments. The coral, clam +coral and clam treatments saw initial increases in abundance followed by declines, but abundance remained higher than the control. Change in species composition was apparent in the coral and clam+coral treatments compared with controls due to increased corallivores (*Chaetodon trifasciatus*, *Chaetodon octofasciatus*, *Chaetodon auriga*), juvenile wrasses (*Halichoeres* sp.), juvenile cardinalfish (*Apogon* sp.) and damselfish (*Amblyglyphidodon curacao*).
Yap, 2009	Lipata Island, Philippines	24	27 (*18*)	Four treatments: (a) natural reef plots, (b) degraded plots with transplanted coral colonies from a nearby source, (c) empty plots and (d) empty control plots situated >100 m away from other treatments.	Significant difference in abundance of all taxa pre and post-restoration at transplant plots. Transplant plots observed an increase in damselfish through time. Fish diversity in transplant plots was significantly higher than in empty control plots.
*Baria *et al.*, 2010	Malilnep Channel, Bolinao, Philippines	19.2	3	Transplanting tiles with settled 6-week old spat of *Acropora tenuis* corals that was reared *ex situ*. Three treatments at two depths: (a) caged, (b) open-sided cage and (c) no cage.	Lower survival of spat in uncaged compared to cage and open-sided cage treatments. No significant difference in survival between closed and open cages indicating that grazers may not have a detrimental effect on spat survival. Significantly higher levels of macroalgae in caged *vs*. open cage and no cage treatments. Qualitative observations of grazing scars on tiles in the uncaged and open-sided cage treatments.
*Nakamura *et al.*, 2011	Okinotorishima, Japan	1.5	22	Juvenile *A. tenuis* corals cultured *ex-situ* from wild colonies. Juvenile fishes introduced to culture tanks to control macroalgal growth. Corals then transplanted to reefs across three treatments: (a) wire cage treatment, (b) uncaged treatment with all corals facing upwards and (c) uncaged treatment with half of the corals facing downward thus benefitting from shade.	Four-fold increase in coral cover in the cage treatment as corals were protected from fish predation. No increase in coral cover in the other treatments. Qualitative observations of coral predation by filefish *Cantherhines dumerilii* and pufferfish *Arothron meleagris*.

(Continues)

TABLE 1 (Continued)

Reference	Location	Scale of restoration (m^2)	Length of study (months)	Description of coral restoration methods	Results relating to fish assemblages
Shaish *et al.*, 2010	Santiago Island, Philippines	54	15	The use of weedy coral species *Montipora digitata* in coral gardening was tested, with the transplantation of nursery-reared colonies in low- and high-density designs across two locations.	Qualitative measures of rapid colonisation by juvenile fishes (Chaetodonidae, Pomacentridae, *Halichoeres* sp., *Apogon* sp.).
Villanueva *et al.*, 2010	Malilnep Channel, Bolinao, Philippines	47.46	6 (*4*)	Deployment of concrete reef balls: (a) reef balls with transplanted corals at low density, (b) reef balls with transplants at high density, (c) reef balls without coral transplants. Half the balls in each treatment were stocked with herbivorous *Trochus niloticus* invertebrates which was continuously maintained throughout the study.	No difference in herbivorous fish biomass in any of the three treatments regardless of *T. niloticus* presence/absence.
*Bongiorni *et al.*, 2011	St John & Lazarus Islands, Singapore	22.5	14	Testing the effects of fish farm effluents on coral nubbins. Two coral nurseries were deployed, one of them in vicinity of a fish farm.	Coral survival rates were overall low with survivorship differing among species, and, within each species, between nurseries. Growth of farmed colonies significantly varied among coral species and nursery locations.
Fadli *et al.*, 2012	Pulau Weh, Aceh, Indonesia	325	41	Concrete modules were deployed on sand and rubble habitat. *Acropora subglabra* and *Acropora formosa* coral fragments collected from nearby reefs were attached to the modules.	Reef fish abundance increased exponentially with restoration age, whereas species diversity increased linearly. Qualitative observations of pelagic predators, such as *Caranx melampygus*, attracted to the structures.
*Forrester *et al.*, 2012	White Bay, Guana Island, British Virgin Islands	Not reported	36	Transplant stress was evaluated in (a) recently transplanted *Acropora palmata* corals, (b) established transplants and (c) non-transplants. Coral fragments inside and outside damselfish *Stegastes planifrons* territories were compared.	Coral bleaching and tissue loss in new and established transplants were not significantly different inside and outside damselfish territories. Primary suspected causes of tissue loss at the restoration site were white syndrome and damselfish bites, the latter leading to coral mortality in 40% of established transplants and 19% of newly transplanted colonies. Damselfish did not preferentially target new transplants. Focal parrotfish rarely attacked *A. palmata* fragments.
Mbije *et al.*, 2013	Unguja & Mafia Island, Tanzania	216	24 (*12*)	A variety of nursery-reared coral colonies were transplanted onto reefs denuded from bleaching.	Fish assemblage composition was significantly altered through restoration time at the Mafia Island site but not at the Unguja Island site.
Merolla *et al.*, 2013	Guana Island, British Virgin Islands	Not reported	84 (*23*)	Elkhorn coral fragments transplanted at a single site across 7 years.	Three-spot damsel recruits increased over the last 3 years of the project. All recruits initially settled on transplanted elkhorn corals, but 57% of recruits settled on other microhabitats by end of study. Three-spot damselfish recruits positively selected for larger coral transplants. Recruits on elkhorn corals had higher survival than those on other substrata, but this was not statistically significant.

TABLE 1 (Continued)

Reference	Location	Scale of restoration (m^2)	Length of study (months)	Description of coral restoration methods	Results relating to fish assemblages
dela Cruz *et al.*, 2014	Santiago Island, Bolinao, Philippines	96	19 (*19*)	*Acropora intermedia* and *Acropora pulchra* fragments transplanted in low and high densities on sandy and rubble substrate.	Fish abundance increased by 50% on high density compared to low density and control plots. Fish species richness was higher at transplanted plots than at controls, but there was no difference between the two densities. Fish composition remained similar between all treatment plots. Fish biomass was significantly higher in the high-density plots than in the low-density and control plots.
*Frias-Torres *et al.*, 2015	Cousin Island Special Reserve, Seychelles	108	27 (*8*)	Three midwater net nurseries were deployed with attached coral fragments of mixed species. Nursery-associated fish assemblages were investigated with GoPros following a 20-month growth period and 7 months post-coral harvesting.	Transient and resident reef fishes across six families were observed feeding at nurseries. Fish decreased after coral harvesting, with only two transient (*Platax teira*, *Bolbometopon muricatum*) and two resident species (*Neopomacentrus cyanomos*, *Pomacentrus caeruleus*) remaining at nurseries. Density of *P. caeruleus* was 12–16 × higher when corals were present than after coral harvesting. Higher abundance of large fish resulted in 2.75 × less hours spent in nursery cleaning.
*Frias-Torres & van de Geer, 2015	Cousin Island Special Reserve, Seychelles	Not reported	5	Animal-assisted cleaning of biofouling tested on nursery corals prior to transplantation. Cleaning stations of nursery ropes with attached corals were placed at transplantation and nursery sites.	32 fish species across eight families and four trophic levels were observed feeding at the transplantation site, whereas only one species was observed interacting with the structure at the nursery site. Qualitative observations of *Balistoides viridescens* feeding on rope barnacles. Fish-related coral predation was absent at both sites.
*Horoszowski-Fridman *et al.*, 2015	Gulf of Eilat, Israel	2.4	17.5	Coral survival and performance were compared between: (a) nursery-farmed colonies of *Stylophora pistillata* and *Pocillopora damicornis* corals, (b) wild colonies and (c) colonies maintained at the coral nursery.	Intense corallivory by Scaridae and Chaetodontidae fish species caused major tissue loss particularly in transplanted *Stylophora* coral fragments with more bites than on corals at controls. Attacks on *Pocillopora* transplants were comparable to those on native corals. Percentage of coral colonies damaged by fish gradually increased over time in transplanted and wild colonies. Mortality was not linked to fish predation; nonetheless, fish attacks were important factors in coral detachment. Corallivory was minimal at the nursery for both coral species.
*Schopmeyer & Lirman, 2015	Florida Reef Tract, U. S.	150	12 (*12*)	Transplantation of nursery-reared *A. cervicornis* colonies. Small additional coral thickets also transplanted.	Outplant survival was high and damselfish occupation rate low and size-dependent. Territorial damselfishes selected larger, more complex coral colonies. Most algal lawns were established within 6 months of transplantation. All coral thickets transplanted near three-spot damselfish territories were colonised and defended within 6 months, with lawns covering 20%–45% of coral colonies. Damselfish occupation reduced coral predation by other corallivores.
*Xin *et al.*, 2016	Tioman Island, Malaysia	33.6	14	Transplantation of *A. formosa* coral fragments collected at a nearby island onto a PVC frame nursery, secured to the substrate.	Higher mortalities at the nursery site than on natural reef were attributed to predation by fish and other corallivores. Qualitative observations of bite marks. High variation in predation at nursery site but relatively constant on natural reef.
*Huntington *et al.*, 2017	Tallaboa, Puerto Rico	70	108 (*24*)	Natural and restored (coral nurseries and transplantation) *A. cervicornis* reefs.	Partial coral mortality induced by corallivores was low at the restored site (0.15% damselfish induced). No evidence of facilitation between high coral densities and fish metrics at the restored site, potentially due to low overall coral densities or depleted fish populations.

(Continues)

TABLE 1 (Continued)

Reference	Location	Scale of restoration (m^2)	Length of study (months)	Description of coral restoration methods	Results relating to fish assemblages
*Lohr *et al*., 2017	Little Cayman, Cayman Islands	24	43.8 (*2.8*)	Nursery-reared *A. cervicornis* fragments transplanted alongside wild coral populations along a depth gradient.	Wild *Acropora* colonies experienced *Stegastes* spp. predation particularly at intermediate depth. No *Stegastes* spp. predation occurred on outplanted colonies.
Ng *et al*., 2017	Kusu, Lazarus, Subar Laut, Subar Darat, Satumu & St John's Islands, Singapore	44	168	Monitoring of established fibreglass artificial reef modules deployed in the early 2000s.	Qualitative observations of fishes (Labridae, Pomacentridae) taking shelter within the module cavities as well as the presence of fish eggs.
Opel *et al*., 2017	St. Croix, US Virgin Islands	32	10 (*7*)	Before After Control Impact study design with nursery-reared transplanted *Acropora cervicornis* colonies.	Mean fish abundance was higher in outplants than in controls despite a decrease in abundance 2 months post-outplanting. Species richness was higher in outplants than in controls. Little similarity in fish assemblage composition between outplants and controls shortly post-outplanting. By end of study both outplants had no overlap with controls or with each other. Key species accounting for dissimilarity were *Thalassoma bifasciatum*, *Sparisoma aurofrenatum*, *Gnatholepis cauerensis* and *Stegastes partitus*. *T. bifasciatum*, *S. aurofrenatum* and *S. partitus* were more abundant in outplant plots, whereas *G. cauerensis* were more abundant in controls.
Taira *et al*., 2017	Lazarus Island, Singapore	500	36 (*0.03*)	Coral table nurseries *vs*. nearby natural reef.	Juvenile *C. octofasciatus* density at the nursery was twice that of natural reef despite similar coral densities. Adult and competing territorial damselfishes only recorded at natural reef.
*Page *et al*., 2018	Florida Keys, U.S.A.	0.2	31	Slow-growing coral micro-fragments and large fragments of *Orbicella faveolata* and *Montastrea cavernosa* were outplanted using epoxy. Outplanting locations included a nearshore and offshore site. Corals were collected and maintained in the laboratory prior to transplantation.	Little evidence of predation (fish+other predators) on larger fragments for the whole study, whereas heavy predation was observed on microfragments, particularly at the offshore site. Predation scars were no longer observed 3 months post-transplantation. Significant influence of predation on survival of *O. faveolata* microfragments within the nearshore site; when a microfragment lost >40% of tissue from parrotfish predation, there was 0% chance of survival. This relationship was not observed for *M. cavernosa* fragments at the nearshore site or either coral species at the offshore site.
*Knoester *et al*., 2019	Wasini Island, Kenya	45	3.3 (*3.3*)	Uncaged, caged and cage-control treatments, each composed of nursery trees with attached *Acropora verweyi* fragments. Caged treatments isolated fish from coral, whereas cage-control treatments had side openings so fish could enter the structures.	Herbivory was lowest and fouling highest in the caged treatment with >100-fold increase in macroalgae. Grazing on nursery structures was dominated by surgeonfish *Ctenochaetus striatus*. The most abundant herbivores were territorial damselfish *Plectroglyphidodon lacrymatus*, *C. striatus* and the surgeonfish *Naso brevirostris*. ~10% of coral fragments in uncaged and cage-controls were bitten by corallivores. Fouling control by herbivory outweighed costs of corallivory.

TABLE 1 (Continued)

Reference	Location	Scale of restoration (m^2)	Length of study (months)	Description of coral restoration methods	Results relating to fish assemblages
Ladd *et al*., 2019	Florida Keys National Marine Sanctuary, U.S.A.	Not reported	132 (2)	Restoration sites of varying coral transplant densities and maturity. Coral transplants originated from nearby nurseries.	No differences in species richness or diversity between restored and control sites and no within-reef differences in total biomass. Damselfish occurred at 1.5 × higher densities in restored sites than controls with no differences in abundances of any other fish taxa. Restoration did not influence density of juvenile fishes. Mixed evidence that herbivory and corallivory varied with restoration regimes.
McLeod *et al*., 2019b	Whitsunday Islands, Australia	Not reported	16 (1)	Cyclone-displaced, moderately sized *Porites* spp. colonies transplanted to reef. Coral "bommies" (1–3 m Ø) had been displaced to intertidal reef flats and were subsequently repositioned.	Species of reef fish across eight genera were interacting with the restored bommies. Damselfishes were the most abundant, in particular *Neopomacentrus bankieri* and *Pomacentrus wardi*. Roving herbivores, particularly *Acanthurus grammoptilus*, *Siganus doliatus* and *Scarus rivulatus* were observed grazing on the bommies and surrounding substrate limiting algal turfs and macroalgae. Parrotfish grazing scars were observed on all surveyed bommies.
*Williams *et al*., 2019	Badi Island, Indonesia	7000	30	Small modular open structures were deployed to stabilise rubble and to support wild-collected and nursery-reared transplanted coral fragments.	Removal of algal-farming territorial damselfishes, especially *Dischistodus perspicillatus* and *Neoglyphididon crossi*, was necessary to prevent algal overgrowth in the first weeks post-deployment (qualitative). Qualitative observations of rabbitfishes, parrotfishes, and surgeonfishes rapidly colonising restored sites.
Jayanthi *et al*., 2020	Vaan Island, India	26,500	38 (36)	Artificial reef modules made of steel-reinforced cement were deployed on the side of Vaan Island. Side openings and holes permitted water flow.	Fish density and species richness increased over the study. *Lujanus*, *Pempheris*, *Chaetodon* and *Scarus* species were commonly encountered around the artificial reefs.

Note: These studies were identified by systematic searches conducted in Jan/Feb 2020 in Web of Science. Keywords used in the searches are given in Table S1 (supporting information). This approach was complemented with searches in Google Scholar, hand-searching reference lists of included studies and by screening the recently compiled database of coral reef restoration studies in Boström-Einarsson *et al*. (2020). Artificial reef publications that (a) did not aim to mimic natural reefs (*i.e*., shipwrecks, jetties, breakwaters), (b) had the primary goal of increasing fishing productivity rather than ecosystem rehabilitation and (c) solely investigated ecological processes (*i.e*., succession, predation) without clear restoration aims were excluded from this review.

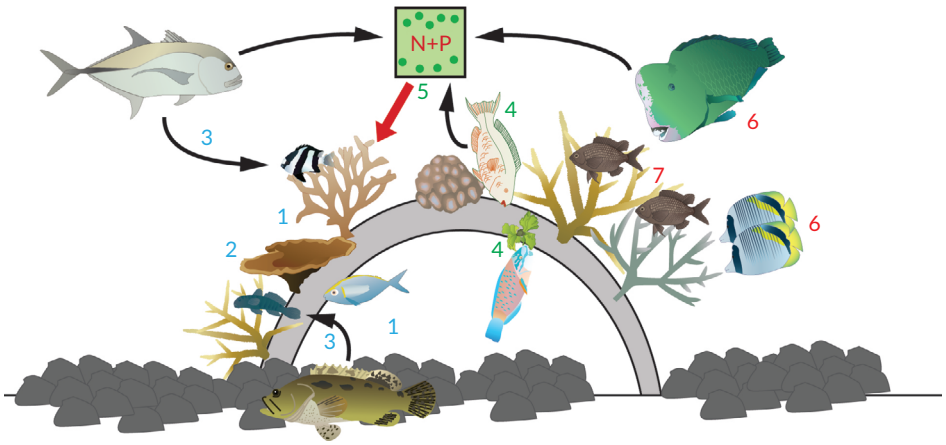

FIGURE 1 Summary of interactions between fishes and their restored coral reef habitat. Benefits for fishes include the introduction of complexity for reef-associated fish species that provides shelter for reef-associated species either under artificial structures or within coral transplants (1), which is enhanced by providing transplant species with a range of morphologies, densities and shade-producing properties (2). Fishes will also benefit from increased food sources including coral (2) and other fishes (3). Through these trophic interactions, fishes play positive roles in restoration projects including herbivory to control algae growth (4) and provision of nutrients for coral growth (5), but may also have negative impacts through coral predation (6), and damselfish territories (7)

provision is considered (Bohnsack & Sutherland, 1985). In several studies deploying artificial reefs consisting of concrete blocks, the complexity of the blocks including the presence and size of holes within the structures had a significant effect on colonising fish assemblages (Hixon & Beets, 1989; Hixon & Beets, 1993; Sherman *et al*., 2002). Vertical topography has also been shown to have a significant effect on fish assemblages, with vertical jetty pillars experiencing much higher recruitment than low-relief natural reefs in the Red Sea (Rilov & Benayahu, 2000). Artificial reef design and the presence of holes and cracks providing protection for prey also seem to be particularly important in defining predatory fish assemblages (Da Rocha *et al*., 2015; Gregalis *et al*., 2009; Spieler *et al*., 2001). For example, in an experimental study where artificial reefs containing varying shelter sizes were deployed, smaller shelters were effective in excluding large predators, whereas the presence of larger holes increased the abundance of large piscivores and indirectly reduced prey numbers (Hixon & Beets, 1989). This work provides potential guidance for the spacing and coral growth forms that might most benefit fishes, along with a recognition that complexity occurs at multiple scales (Harborne *et al*., 2012b).

The provision of shade in addition to physical shelter provided by reef crevices and holes is also likely to be a contributing factor in attracting fish assemblages to restored reefs (Spieler *et al*., 2001). Increasing complexity by reintroducing intricate and table-shaped corals may produce areas of shade in which juvenile and nocturnal coral fishes can take cover (Hair *et al*., 1994; Kerry & Bellwood, 2016; Sheppard, 1981; Stimson, 1985). Provision of shade may effectively conceal vulnerable fishes while allowing them to better spot predatory threats (Helfman, 1981), and shade may provide protection from the damaging effects of UV light (Kerry & Bellwood, 2015b). Kerry and Bellwood (2012) investigated fish interactions with different coral morphologies and observed a significant preference of large fishes for tabular-shaped corals with opaque canopies when compared to branching and massive colonies. In a later experimental study (Kerry & Bellwood, 2015a), the exclusion of fishes from large tabular corals significantly altered fish assemblages despite tabular corals only occupying a small percentage of the total benthic cover. If shade-providing corals act as keystone structures on healthy reefs, then it becomes important to consider a selection of coral species and morphologies for transplantation for attracting diverse and abundant fish assemblages (Table 2; Edwards, 2010; Shaver & Silliman, 2017). For example, often branching coral forms are chosen for transplantation because of their faster growth and survivorship (Barton *et al*., 2017; Epstein *et al*., 2001) which, while increasing overall complexity, may limit the provision of shade. Different fish species are likely to be attracted to separate coral morphologies, and although slow-growing massive species tend to be less attractive to fishes, they are less likely to succumb to disease and bleaching (McCowan *et al*., 2012). Shade may also be provided by any artificial structures to which corals are attached. Currently, the understanding of the impact of shade on various coral reef fishes is incomplete, and in addition, no research has attempted to evaluate the benefits of shade in the context of coral reef restoration (Table 1), despite the importance of specific physical structures in driving fish assemblages.

Coral density and connectivity between coral fragments may also significantly shape resident fish assemblages as clumping of coral colonies may be particularly appealing to aggregating fishes (Edwards & Gomez, 2007; Griffin *et al*., 2015; Huntington *et al*., 2017; Ladd *et al*., 2016). Ensuring individual fragments or colonies are not too isolated may be vital in supporting prey fish assemblages as large open spaces are likely to increase predator densities (Stewart & Jones, 2001). Whereas outplanting corals at high density has been linked with increased fish abundance and biomass (dela Cruz *et al*., 2014), densely packed corals can exclude herbivores and promote algal growth between fragments (Shafir *et al*., 2006). Rubble-dwelling fishes, such as certain Pinguipedidae and Gobiidae species,

TABLE 2 Summary of the interactions between natural reefs and fishes and how this information can be used to optimise the recovery of fish assemblages in reef restoration efforts

Coral reef concepts		Reef restoration recommendations
Introducing habitat complexity	High complexity corals provide shelter opportunities for prey items, *e.g.*, juvenile fishes, cryptic fishes and invertebrates, reducing predatory success.	Restoration must increase complexity, providing shelter to support fish communities. This can be incorporated through man-made structures and/or by the transplantation of intricate corals.
	Increased refuges may enhance prey fish numbers providing more opportunities for predators. Small holes provide shelter for prey; large holes increase predator abundance.	Varying levels of complexity should be introduced; high complexity will provide shelter for prey fishes, but inclusion of gaps and moderate coral transplantation densities will ensure large-bodied predator success.
	Shade-producing corals offer shelter to juvenile and nocturnal fishes as well as protection from UV light. Tabular corals shape fish assemblages even when occupying a small proportion of total coral cover.	The provision of shade needs to be included when designing restoration structures. Some shade-producing tabular corals should be introduced in addition to the more popular branching corals.
	Connectivity with other ecosystems will greatly affect fish abundance and biomass.	Where possible, reef restoration projects should be set up close to mangrove and seagrass habitats to enhance fish populations through provision of nursery and foraging areas.
Role of herbivorous fishes	Algae competes with corals for space and will opportunistically overgrow, shade or abrade coral colonies that are vulnerable or damaged.	Surveys to ensure sufficient herbivorous fishes are present are recommended prior to restoration. Removal of macroalgae may be necessary during initial stages while healthy grazing populations of fishes establish.
	Grazing may be enhanced with various management practices such as fishing reductions.	Where possible, restoration projects should be located in marine reserves or at locations supporting a high biomass and diversity of grazers from various functional groups.
	Territorial damselfishes can have deleterious effects on vulnerable coral colonies by biting coral polyps to promote algal growth. They are particularly attracted to fast-growing branching coral colonies.	Surveys of territorial damselfish and their known predators should be carried out prior to restoration to determine whether damselfish removal is required. A variety of coral morphologies should be transplanted to help minimise damselfish effects.
Nutrient provision	Aggregating fishes supply nutrient-limited corals with added excretory products. Coral morphologies that promote low water flow between branches retain these nutrients more effectively.	In line with transplantation of varying coral morphologies, corals with closed morphologies should be included to enhance nutrient absorption and coral growth.
	Fish farms may provide a source of natural enrichment.	Consideration should be given to setting up coral nurseries near fish farms as nutrients may stimulate fragment growth. Nonetheless, this needs to be assessed alongside surveys of herbivorous fish populations, as algal overgrowth remains one of the main concerns on nutrient-enriched, coral-poor reef restoration sites.
Corallivory	Herbivores may induce coral recruit mortality through accidental grazing, and corallivores will target juvenile corals through predation.	Where corallivory is a problem, rearing juvenile corals to larger sizes *ex-situ* prior to transplantation is recommended to decrease size-dependent mortality.
	Corallivores may be selective in their coral preferences. Nevertheless, the positive effect of the cropping of algae by herbivores appears to outweigh the negative effect of occasional predation by herbivorous and corallivorous fishes.	Surveys to establish the presence of corallivorous fishes are recommended prior to restoration. Outplanting a range of coral species and morphologies could minimise the impact of corallivores.
Predatory fishes	Predatory fishes have a vital role in maintaining healthy coral reef ecosystems and supporting fisheries.	Attraction of predator assemblages should be a key aim of restoration projects. Although it may be difficult to identify specific mechanisms for this at the start of a restoration project, surveys of predatory fish populations over restoration time are recommended to inform this aim.
	Marine-protected areas and reserves, even of small size, can have significant positive impacts on predatory species through the prevention of fishing activity.	Where possible, setting up coral restoration projects within established protected areas will increase their likelihood of success due to the protection of predatory species.

often recruit to reefs post-disturbance and may be heavily impacted by subsequent increases in coral cover associated with restoration (Coker *et al*., 2012; Opel *et al*., 2017; Syms & Jones, 2000). Furthermore, artificial patch reefs with small-scale isolation have observed increased fish abundance, species richness and juvenile recruitment when compared to continuous reefs (Belmaker *et al*., 2011; Schroeder, 1987). Patch reef designs may, therefore, be preferable for reef restoration, providing a range of habitats and encouraging the recruitment of both coral and rubble-associated species. In addition, connectivity with adjacent ecosystems on a larger spatial scale is an important consideration as many coral fishes migrate between different habitats with the presence of nearby resources, such as nursery

habitats, heavily impacting fish biomass (Mumby *et al*., 2004; Nagelkerken *et al*., 2000; Nagelkerken *et al*., 2002; Ogden & Quinn, 1984). For example, juvenile fishes may have entirely different refuge needs to adults and could greatly benefit from the presence of mangrove or seagrass nursery and foraging habitats near restoration sites. It is therefore essential that an integrated planning approach is taken at the design stage of restoration projects to maximise benefits to fish by considering small- to large-scale physical characteristics of the habitat and seascape (Table 2).

2.1 | Cryptic species

Although the need to provide shelter for ecologically and economically important fishes by using appropriate restoration design is well known, cryptic fishes are rarely considered in the context of reef restoration (Table 1). Though not primary targets of restoration, cryptobenthic fishes, or more commonly termed "cryptic" fishes, have an important role in reef assemblages and significantly contribute to fish abundance and diversity but are understudied (Ahmadia *et al*., 2012; Brandl *et al*., 2018; Depczynski & Bellwood, 2004; Harborne *et al*., 2012a). As they constitute common prey for piscivorous primary and secondary consumers and supply a substantial amount of energy to higher trophic levels (Brandl *et al*., 2018, 2019; Depczynski & Bellwood, 2003), it is important that they are considered in the context of rebuilding food webs on restored sites. Cryptic species differ from more conspicuous species; they are small (<5 cm), have limited mobility and predominantly live in well-protected cavities formed within coral reef structures (Depczynski & Bellwood, 2003). Consequently they typically have high site fidelity and are affected by a range of physical characteristics, including habitat complexity and shelter quality (Depczynski & Bellwood, 2004; Kobluk, 1988; Prochazka, 1998; Syms, 1995; Willis & Anderson, 2003). Cryptic species specialising in living within coral habitats are likely to be positively affected by the increase in structural complexity and live coral cover through the transplantation of stony corals, and the introduction of structures to which they are attached (Jaap, 2000). Indeed, the introduction of artificial reefs has previously increased the abundance of small fishes such as cardinalfishes and gobies (Clark & Edwards, 1999; Thanner *et al*., 2006). Without a fuller understanding of the impact of reef degradation on cryptic species, any potential positive effects of restoration on this group of fish species will be difficult to manage or monitor. Further research is critical to explore cryptic fish population structures across different restoration designs, and how they may aid the recolonisation of higher trophic species.

3 | THE ROLE OF HERBIVOROUS FISHES

Herbivorous fishes are vital for reef restoration programmes; sufficient grazing is a necessity to prevent algae from smothering coral fragments and outcompeting coral transplants, particularly during the early stages of restoration (Edwards, 2010; Edwards & Gomez, 2007). Macroalgae rarely overgrow thriving coral colonies. Nonetheless, when coral colonies are already damaged or dead, algae can colonise in an opportunistic manner (McCook *et al*., 2001), overgrow coral recruits (Box & Mumby, 2007), and algae may also act as disease vectors (Nugues *et al*., 2004), so that the control of macroalgal cover by grazing fishes is vital. Small coral fragments are particularly susceptible to sub-lethal effects from contact with macroalgae (Ferrari *et al*., 2012). This susceptibility is particularly relevant for restored coral colonies where coral fragments may be small and are already stressed due to the transplantation process. Research conducted at several restoration sites within the Florida reef tract found high cover of macroalgae to be a major threat to the survival of *A. cervicornis* fragments (van Woesik *et al*., 2018). Indeed, reef restoration is not recommended in areas where grazing populations of fishes and/or invertebrates are scarce as this would prevent restored corals from recruiting in the future, therefore rendering the exercise futile (Edwards, 2010). Surveys of existing fish populations at proposed sites are, therefore, essential (Edwards & Gomez, 2007), and the active removal of macroalgae has been suggested on reefs with reduced herbivory in association with coral reef restoration efforts to improve chances of coral survival while coral fragments establish (Ceccarelli *et al*., 2018).

Most reef restoration projects are expensive and require extensive time spent cleaning algae from introduced structures such as coral nurseries (Frias-Torres & van de Geer, 2015) and artificial reef modules (Williams *et al*., 2019), often due to the lack of healthy herbivorous fish populations. With their fused beaks, parrotfishes are particularly efficient at removing algae, consequently freeing up space for coral recruits and reducing coral–algal interactions (Abelson *et al*., 2016b; Bellwood *et al*., 2004; Ogden & Lobel, 1978), either through targeting algae directly (Adam *et al*., 2018) or indirectly while feeding as microphages (Clements *et al*., 2017). Although seemingly less clear in the Pacific (Russ *et al*., 2015), in the Caribbean there are evident relationships between parrotfish biomass and the abundance of large-sized individuals with macroalgal cover (Shantz *et al*., 2020; Williams & Polunin, 2001), and consequently restoring parrotfish populations is often the focus of conservation initiatives in the western Atlantic (Jackson *et al*., 2014). Nonetheless, it is necessary to rebuild the entire herbivorous fish guild, including macroalgae-eating browsers to keep algae communities in an early successional stage (Adam *et al*., 2015; Burkepile & Hay, 2010; Cheal *et al*., 2010). For example, the reversal of an experimentally induced algal phase shift was attributed to the batfish *Platax pinnatus* (Linnaeus 1758), a species not previously classified as a conventional grazer, whereas grazing from parrotfishes and other key herbivorous species had little impact on direct removal of macroalgae (Bellwood *et al*., 2006). Additional fishes within the herbivorous guild continue to be identified in both the Pacific and Caribbean faunas (Tebbett *et al*., 2020). Non-fish species such as urchins are also functionally important grazers on many reefs (Edmunds & Carpenter, 2001); thus, a diversity of fish and invertebrate grazers is advocated to promote restoration success.

In an marine protected area (MPA) at Cousin Island in the Seychelles, coral fragments were set up to grow at a coral nursery site located near a healthy local reef, aiming to reduce cleaning costs

during the first phase of coral gardening prior to coral transplantation. The presence of reef fishes removing the nursery of biofouling organisms, such as algae and invertebrates, reduced the usual cleaning time by 60% (Frias-Torres *et al*., 2015). This trophic facilitation has significant implications for coral reef restoration projects in terms of cost-effectiveness (Toh *et al*., 2013). During a different study at the same MPA, restoration structures were filmed to investigate the importance of grazers and to test a novel cleaning station technique (Frias-Torres & van de Geer, 2015). Within 48 h of nursery rope structures being placed at the experimental site, all biofouling reef algae had been removed by herbivores, therefore eliminating the need for maintenance-cleaning and the risk of coral shading by macroalgae. The benefits herbivorous fish species provide by reducing algal competition are thought to outweigh any damage to juvenile coral recruits and coral fragments caused by intense grazing activities (see also the section "Corallivory"), at least on natural reefs (Mumby, 2009). Moreover, grazing opens new settlement space for coral larvae to colonise (Doropoulos *et al*., 2016), thus facilitating natural ecological recovery processes.

Although the reduction in fishing pressure to protect herbivorous fish stocks is often a key management step to increase reef resilience, the enhancement of grazers has also been proposed as a complementary method to reef restoration (Abelson, 2006). Typically this is achieved through marine reserves, but region-wide fishing bans on herbivores are increasingly being utilised (Cox *et al*., 2013; O'Farrell *et al*., 2015). Although the recovery of parrotfishes can be rapid (<5 years, O'Farrell *et al*., 2015), the re-introduction of grazers by releasing fish larvae on restored, but recruitment-limited, reefs has been suggested as a useful management technique in accelerating stock recovery and increasing herbivory (Abelson *et al*., 2016b). In a modelling study, different simulated scenarios of fish stock enhancement predicted that fish restocking could substantially increase the success of coral reef restoration projects. Restocking was shown to lead to enhanced coral cover and grazing fish density while reducing macroalgal cover in a significantly shorter amount of time when compared to restoration without restocking interventions (Obolski *et al*., 2016). Nonetheless, restocking remains a logistically challenging management option, and field tests are lacking. For example, post-settlement mortality of fish larvae needs to be addressed before attempting restocking activities, as restored reefs with limited food or shelter from predators may not be adequate for supporting juvenile communities (Almany & Webster, 2006; Booth & Hixon, 1999; Forrester, 1990; Juanes, 2007).

Most fish and coral restoration interactions are considered to be beneficial; nonetheless, certain fish species are known to have deleterious effects on restoration success and create considerable challenges for reef managers (Forrester *et al*., 2012). Herbivorous damselfishes are well known for their effects on coral colonies, and are often among the first fish groups to colonise restored reefs (Schopmeyer & Lirman, 2015). Within their territories, damselfishes may intentionally bite and damage live coral polyps to promote the growth of the algae they consume on the coral skeleton (Ogden & Lobel, 1978), which becomes a major issue on restoration projects where coral fragments are already fragile (Ladd *et al*., 2018; Williams *et al*., 2019; Table 1). For example, *Isopora palifera* colonies transplanted within territories of the white damsel *Dischistodus perspicillatus* (Cuvier 1830) eventually died due to the metabolic cost of combating algal smothering (Potts, 1977). When coral fragments were transplanted inside and outside Australian gregory (*Stegastes apicalis*) (De Vis 1885) and dusky farmerfish (*Stegastes nigricans*) (Lacepède 1802) territories, transplant mortality was higher inside the territories than in control areas (Casey *et al*., 2015). Schopmeyer and Lirman (2015) studied the effects of territorial damselfish on a coral reef restoration project in Florida. Immediately following, and even during, the outplanting of nursery-reared *A. cervicornis* colonies, damselfishes colonised the restored sites and established algal mats within the first 6 months with large coral colonies experiencing up to 45% colony mortality. Williams *et al*. (2019) found that after the first few weeks of coral transplantation, it was critical for coral survival that the large *D. perspicillatus* and Cross's damsel *Neoglyphidodon crossi* Allen 1991 were actively managed to prevent algal overgrowth.

Although algal-farming by damselfishes is a natural ecological process on coral reefs, locating restoration programmes in areas where predators of damselfishes are present in higher densities (*e.g*., MPAs) may mitigate the negative effects of algal farms through predation and indirectly reduce the incidence of coral disease (Vermeij *et al*., 2015). The removal of territorial damselfishes (Casey *et al*., 2015; Schopmeyer & Lirman, 2015) may also help to ensure their presence does not compromise restoration success (Table 2). Transplanting a diversity of coral species is likely to be beneficial and may additionally minimise the impact of damselfishes. A prevalence of fast-growing branching corals may attract damselfishes away from slower-growing corals that may be less able to compete with algal growth stimulated by damselfish gardening. It is, however, important to note that impacts will vary depending on geographic location and damselfish species. Although territorial damselfishes are a significant challenge to coral reef restoration efforts, particularly in the Caribbean, their effects are likely to be context-dependent (Ladd *et al*., 2018). For instance on Indo-Pacific reefs, territorial damselfishes can exclude corallivores from their territories (Gochfeld, 2010; White & O'Donnell, 2010), resulting in increased coral growth, diversity (Glynn & Colgan, 1988) and recruitment (Gleason, 1996) in these areas. Understanding the interactions between populations of farming damselfishes, their predators, and whether planting a diversity of coral morphologies can influence the impact of damselfish territoriality during restoration is an important area for future study across a range of geographical locations.

4 | NUTRIENT PROVISION

In addition to herbivory, there are other mutualistic relationships that may benefit restoration activities. For instance, fishes can provide primary producers with some of the nutrients they need through excretion of ammonia and faeces, thus influencing primary production and community structure (Allgeier *et al*., 2013, 2014; Benkwitt *et al*., 2019;

Burkepile *et al*., 2013). Coral reefs are primarily nutrient-limited, and yet they are some of the most productive ecosystems on the planet (Davis *et al*., 2009; Szmant-Froelich, 1983). Fish communities store and supply substantial quantities of nitrogen and phosphorus in the form of excretion and egestion (Allgeier *et al*., 2017). This nutrient source is crucial in supporting coral reef productivity (Allgeier *et al*., 2014; Holmlund & Hammer, 1999), and will increase with increasing fish abundances on restored reefs. Nutrients may be translocated from other sources such as seagrass beds as coral fishes forage on adjacent habitats during the night but return to shelter in coral colonies during the day, thus creating nutrient hotspots (Meyer & Schultz, 1983). For example, the nutrient-rich gill excretions and phosphorus-rich faeces of grunts were found to increase the growth of *Acropora* and *Porites* coral colonies (Meyer & Schultz, 1985), and high nutrient delivery has been associated with increased herbivorous activity and reduced algal cover on outplanted coral colonies (Shantz *et al*., 2015). Holbrook *et al*. (2008) found a mutualistic relationship between *Pocillopora* corals and yellowtail dascyllus (*Dascyllus flavicaudus*) Randall & Allen 1977 communities, with a positive relationship between fish biomass and coral growth. They suggested that biomass of associated fishes and coral colony openness influenced colony fitness. Colonies that hosted larger numbers of fishes received a better supply of nutrients and grew quicker. Similarly, closed colonies that had limited water flow between branches retained more fish-derived nutrients, thus experiencing enhanced growth. This is relevant when selecting coral colonies for transplantation (see also the section "The Role of Habitat and Seascape Complexity") to maximise potential benefits from such mutualistic relationships while maintaining a high transplant diversity (Table 2).

To date, only a handful of studies have tested the benefit of fish-derived nutrients on restored coral fragments and colonies (Table 1). Bongiorni *et al*. (2003) compared growth and gonad development in coral fragments suspended near a fish farm and in an oligotrophic control site. Despite nutrients potentially being deleterious to corals by enhancing algal growth and increasing water turbidity, Bongiorni *et al*. (2003) found that proximity to the fish farm greatly enhanced growth and reproductive activity of *Acropora eurystoma* and *Stylophora pistillata*. Coral fragment growth rates were 3 to 4 times higher at the nutrient-enriched site, and oocyte numbers were significantly higher, compared to the fragments located at the reference site. Shafir *et al*. (2006) also suggested that placing their suspended coral nursery 10 m from a large fish cage containing gilthead seabream *Sparus aurata* Linnaeus 1758 was instrumental in its success and recommended placing coral nurseries within nutrient-rich environments to enhance coral growth, shorten nursery incubation time and reduce costs and threats of predation and competition. Such benefits may extend to fishes repopulating restored reefs.

The benefits of enhanced nutrient supply by fishes may be context-dependent, as high levels of fish excretions can trigger shifts to algal-dominated states on coral-depauperate reefs as opposed to coral-dominant reefs (Burkepile *et al*., 2013). Furthermore, whereas natural enrichment tends to enhance coral growth, the addition of nutrients by means other than fish-associated processes is not recommended as clear negative associations between anthropogenic nutrient enrichment and coral reef health have been reported (D'Angelo & Wiedenmann, 2014). The differential effects of natural *vs*. anthropogenic nutrients on corals are attributed to a range of distinctions including nutrient identity (ammonium and phosphorus *vs*. nitrate) and concentrations (discrete pulses *vs*. heavy discharge) (Shantz & Burkepile, 2014). Anthropogenic nutrification increases turf algae competition over corals (Vermeij *et al*., 2010) and affects susceptibility of corals to bleaching (Wiedenmann *et al*., 2013). In a field experiment, Zaneveld *et al*. (2016) demonstrated that nutrient pollution can increase coral disease, which was exacerbated at high temperatures, and aggravate the impact of corallivory on coral survival. In their study, although parrotfish predation had a negligible impact on *Porites* coral survival in control plots, coral survival was significantly impacted in nutrient-enriched plots with 92% of *Porites* losing tissue through predation resulting in 62% mortality (Zaneveld *et al*., 2016). Overall, studies on the effects of added nutrients on reefs are conflicting (Koop *et al*., 2001; Lapointe, 1997), and effects are likely to be context-dependent (Mumby *et al*., 2006b; Sotka & Hay, 2009). Thus, further work is required to quantify benefits of fish excretions for coral growth in restoration projects. This could be of particular importance to restoration managers as enhanced fragment growth may reduce the high costs and setbacks associated with coral gardening. Nonetheless, although increased nutrients may stimulate coral growth in some cases, algal overgrowth remains one of the main concerns on coral-poor reef restoration sites (Bowden-Kerby, 2001; Yap, 2004; Young *et al*., 2012).

5 | CORALLIVORY

Corallivorous fishes such as butterflyfishes (Chaetodontidae) can be positively affected by the addition of live coral cover due to increasing food availability (Cole & Pratchett, 2014; Hourigan *et al*., 1988). Taira *et al*. (2017) reported that coral nurseries were adequate habitats for juvenile *Chaetodon octofasciatus*, where their densities were higher than at nearby natural reefs. Predation on coral, while providing an important food source for reef fishes, is however a concern in reef restoration projects, where new coral transplants are particularly vulnerable to native predators and other disturbances (Edwards & Gomez, 2007; Jayewardene *et al*., 2009; Omori, 2005).

Consumers of coral tissue differ in their feeding strategies and effects on coral fitness; butterflyfishes remove single coral polyps without affecting the underlying skeleton. In contrast, parrotfishes, pufferfishes, triggerfishes, filefishes and wrasses also remove part of the underlying skeleton, with a few species acting as bioeroders by actively consuming the dead coral matrix (Rotjan & Lewis, 2008). Therefore, corallivory by reef fishes may adversely affect restoration success. For example, intense corallivory by Scaridae and Chaetodontidae caused major tissue loss and coral detachment in transplanted *Stylophora* coral fragments (Horoszowski-Fridman *et al*., 2015), and high *Acropora formosa* fragment mortalities at a coral nursery site were attributed to severe predation by fish and other

corallivores (Xin *et al*., 2016). The coral-feeding butterflyfish *Chaetodon capistratus* Linnaeus, 1758 was also reported to increase the spread of black-band disease to coral fragments (Aeby & Santavy, 2006).

Although the transplantation of large coral fragments and mature colonies remains the most commonly used method of coral reef restoration, the need for sexually propagated corals has been increasingly recognised (Chamberland *et al*., 2015; Villanueva *et al*., 2012). Outplanting coral juveniles raised from sexually derived larvae, as opposed to using more cost-effective clonal fragments, may help conserve the genetic diversity of restored coral populations (Baums, 2008). Nonetheless, translocating juvenile corals remains challenging as they are particularly at risk of damage from corallivorous fishes (Page *et al*., 2018). For instance, in a study investigating the susceptibility of coral recruits to predation by using settlement plates, parrotfish abundance was correlated with coral recruit mortality, attributed to accidental grazing, whereas butterflyfish abundance was correlated with juvenile coral mortality, attributed to predation (Penin *et al*., 2010). Nonetheless, both survival and growth rates of juvenile corals increase with transplant size and time spent at a nursery prior to transplantation (Guest *et al*., 2014; Ligson *et al*., 2020). Augmenting the size of juvenile corals *ex situ*, thus decreasing size-dependent mortality due to predation, may be preferable when considering optimal transplant size, despite the added maintenance cost (Raymundo & Maypa, 2004; Toh *et al*., 2014).

Baria *et al*. (2010) measured the potential of caging newly transplanted juvenile *Acropora tenuis* corals to reduce post-transplant predation. Juvenile transplants protected by a cage had higher survival rates than the transplants that were not caged. When attempting to mass culture juvenile corals for restoration, Nakamura *et al*. (2011) similarly experimented with coral juveniles placed within cages and without cages. They found that coral growth at the transplantation site was highest when transplants were secured within unshaded cages that protected them from corallivores. Nonetheless, results from a Kenyan nursery site showed that caging fragments significantly increased fouling of corals, creating considerably more damage than occasional corallivory (Knoester *et al*., 2019). Although excluding coral-eating fishes may be beneficial in the early stages of a restoration project, this is often logistically difficult except at small scales (<50 m^2, Table 1) and would also exclude other fishes that remove coral-eating invertebrates such as *Drupella* snails or that reduce macroalgae. The benefit of algal removal by fishes overall appears to outweigh occasional coral damage (Venera-Ponton *et al*., 2011), thus suggesting against the installation of expensive caging apparatus.

Coral species vary in their resistance to grazing, and different coral predators have different prey preferences and feeding modes (Cox, 2013; Hixon, 1997; Rotjan & Dimond, 2010; Rotjan & Lewis, 2008). Studies using natural reef systems have demonstrated selectivity among corallivores (Burkepile, 2012; Roff *et al*., 2011) and where there are fewer palatable coral species corallivory can increase dramatically. Consequently, surveys of existing corallivore species, their dietary preferences and specific tolerances of coral fragments to these species are factors to consider when developing restoration scenarios. The most commonly preyed-upon corals include *Acropora*, *Pocillopora*, *Montipora* and *Porites* species (Rotjan & Lewis, 2008), and introducing alternative coral genera may help mitigate fragment damage. Nonetheless, corallivorous populations have their place on restored reefs as on natural reefs, and thus the transplantation of a broad range of coral species, including a range palatable to corallivores, during restoration would be beneficial. Understanding the food preferences of existing corallivore species would also allow transplantation of some species resistant to coral predation and/or not selected by corallivores to minimise the overall negative impact of corallivorous fish assemblages.

6 | PREDATORY FISHES

There has been a sharp decline in transient apex predator abundance in most reef ecosystems (Baum *et al*., 2003; Essington *et al*., 2006; Jackson *et al*., 2001; Myers & Worm, 2003). Predatory fishes are typically highly valued by fishers, and their densities have been significantly reduced on many reefs, potentially leading to top-down effects (Baum & Worm, 2009; Heithaus *et al*., 2008; Myers *et al*., 2007). For example, predators are important in preventing prey species such as territorial damselfishes from proliferating (Schopmeyer & Lirman, 2015). Corallivorous invertebrates such as the crown-of-thorns starfish (*Acanthaster planci*), the gastropod *Coralliophila abbreviata* and the bearded fireworm (*Hermodice carunculate*) can also negatively affect corals species used in restoration projects (Dulvy *et al*., 2004; Miller *et al*., 2014) unless removed or kept in check by predatory fishes (Ladd & Shantz, 2016; Williams *et al*., 2014). Although predatory fishes play an important regulatory role on restored reefs by reducing predator threats on vulnerable transplanted coral fragments and increasing catches for fishers, they have seldom been investigated in the context of reef restoration, with most of the focus on herbivorous fish populations. Indeed, only a handful of studies have reported the attraction of predatory and transient fish species to restoration sites, and these results have all been qualitative in nature (Salvat *et al*., 2002; Raymundo *et al*., 2007; Fadli *et al*., 2012; Frias-Torres *et al*., 2015; Table 1). This is despite the rebuilding of fisheries being an aim of restoration projects, either explicitly or implicitly. Regardless of local species richness, functional roles on reefs may be performed by only a few species (Hughes *et al*., 2017), thus restoration of functional roles may be a more important goal for the return of top predators than restoration of species diversity *per se*. As the number of restoration projects increases globally, there is an urgent need to assess the impact of different restoration methods on the behaviour of marine predators as some designs, such as biorock-associated electric fields, can deter and reduce their feeding rates (Uchoa *et al*., 2017). Predatory fishes have a vital role in maintaining the ecological balance on reef ecosystems and structuring

coral fish assemblages; therefore, the replenishment of their populations and the maintenance of natural behaviour patterns should remain a priority for restoration projects (Ritchie *et al*., 2012).

With some similarities to coral reef restoration, MPAs and marine reserves aim to maintain ecosystem functions and increase marine habitat quality (Gell & Roberts, 2003; Halpern, 2003; Lester *et al*., 2009), and may provide insight into the effects of restoration on predatory fishes. Coral reef restoration programmes set up within protected areas may reap their combined benefits on fish recovery (Abelson *et al*., 2016a). Several studies have demonstrated that protected areas can have positive effects on fish predators, even in small reserves (Clemente *et al*., 2011; Pilyugin *et al*., 2016; Russ & Alcala, 2004). Therefore, restored and protected coral reefs could provide visitation sites to large transient predatory species (*e.g*., jacks) and territories for resident predators (*e.g*., groupers and eels). It is important to note, however, that reserve benefits to transient species are more likely to be related to protection from fishing and prey availability rather than habitat structure (Roberts & Hawkins, 1997). Nonetheless, some restored reefs also experience a certain degree of protection due to the addition of artificial structures to which the coral fragments are attached, obstructing net-based fishing and thus discouraging certain practices, such as trawling (Edwards & Gomez, 2007). The effect of such protection on stand-alone restoration projects may be limited for wide-ranging species due to the small-scale nature of most reef restoration projects relative to the home ranges of many of the large, high-value predatory fishes (Green *et al*., 2015). A reduction in fishing pressure on large fish species, alongside coral transplantation efforts, is obviously recommended to aid restoration of functional ecosystem food webs.

Although increased habitat complexity influences the abundance of small-bodied resident predators, and to some extent the abundance of transient predators (see the section "The Role of Habitat and Seascape Complexity"), it is more likely that the increase in prey abundance will be the main attractant to piscivorous fishes with large home ranges (Grossman *et al*., 1997; Newman *et al*., 2006; Wickham *et al*., 1973). If reef fish and invertebrate densities benefit from restoration, foraging opportunities for predators will increase in the long term. Habitat complexity may also affect the hunting efficiency of reef predators, but this is largely unexplored. Several recent studies investigating the effect of reef degradation on predators have highlighted a higher abundance and diversity of reef piscivores on recovering reefs compared to degraded reefs due to the availability of higher-quality prey (Hempson *et al*., 2018a, 2018b). On degraded reefs predators feed lower down the food chain, potentially leading to lower nutrition, survival, fecundity and growth (Hempson *et al*., 2017). Reef restoration may, therefore, be able to reverse the effects of trophic downgrading by increasing prey availability and improving predator diet. As most restoration projects ultimately aim to restore top-down trophic interactions and positively affect species of commercial importance, research is urgently needed to understand the factors which will influence the return of large piscivorous fishes. A comparison of foraging success by predators with differing prey pursuit or ambush behaviours on restored reefs would be worth examining, particularly in relation to reef design.

7 | CONCLUSION

This review considers fish–benthic interactions in the growing field of reef restoration research, which has received much less attention than research on effective outplanting of corals, and a number of immediate questions for future research are highlighted (Table 3). In expanding these research questions for coral reef restoration, it is suggested that there is an initial requirement to first understand whether restoration projects can return fish assemblages to their original species composition, or whether restored reefs are likely to support altered or novel fish assemblages. Such altered fish assemblages may function in

TABLE 3 Future key research questions surrounding the recovery of fish assemblages in coral reef restoration efforts

Key research questions	
Introducing habitat complexity	Through what mechanisms does the level of habitat complexity generated by coral transplantation affect both consumptive and non-consumptive predator–prey interactions during the process of rebuilding fish assemblages?
	How important is shade provision in facilitating the return of fish assemblages on restored reefs?
	How does reef restoration design influence the abundance and diversity of cryptic species?
Role of herbivorous fishes	As a key ecological process, how does herbivory of different species (specifically grazing intensity) change on a restored reef over time?
	How can the diversity of coral transplant morphologies be manipulated to reduce the detrimental impact of territorial damselfishes?
Nutrient provision	How can the known benefits of fish excretions on coral growth be utilised to benefit reef restoration projects, in particular coral gardening?
Corallivory	How does food preference of existing corallivore fishes affect restoration success?
Predatory fishes	How can reef design (*e.g*., spacing and a variety of coral transplants) be altered to encourage the return of large predatory fishes?
	What is the relationship between specific reef designs and the different predatory behaviours they facilitate, *e.g*., ambush, pursuit?
Over-arching questions	Which key factors influence whether restoration projects return fish assemblages to their original species composition or generate conditions likely to support novel fish assemblages?
	How do patterns of fish recovery vary with biophysical gradients and across biogeographic regions?

different ways to natural reefs (*e.g.*, different predator–prey interactions). The timeframe over which these changes occur also warrants attention and therefore should be reflected in the monitoring of restored reefs. On healthy reefs, specific guilds of fishes can have both positive and negative effects on corals, and this is also true for restored reefs. Understanding these interactions is likely to be critical in large-scale efforts to increase coral cover through transplants.

With the global challenges currently facing coral reefs, the requirement to explore their restoration has never been greater. Furthermore, it may not be possible to fully restore reefs to pristine conditions, creating a pressing need to understand the novel reef ecosystems that arise through restoration. Irrespective of whether original species composition and diversity are attainable, understanding the interactions between coral restoration and fish assemblages will be vital to ensure that anthropogenically manipulated reef ecosystems still function and provide ecosystem services. Much work has been focused on the benthic component of reef restoration, although very little is known concerning the impact of restoration on fish assemblages in the short and long-term, a clear omission given the integrated relationship between fishes and their reef habitat. As a greater understanding of the interactions between reef restoration and fishes is gained, and as fish-focused research is integrated into the core of restoration efforts, the effectiveness of this important management tool will increase significantly.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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