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Optimizing coral reef recovery with context-specific management actions at prioritized reefs

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ABSTRACT

Assisting the natural recovery of coral reefs through local management actions is needed in response to increasing ecosystem disturbances in the Anthropocene. There is growing evidence that commonly used resilience-based passive management approaches may not be sufficient to maintain coral reef key functions. We synthesize and discuss advances in coral reef recovery research, and its application to coral reef conservation and restoration practices. We then present a framework to guide the decision-making of reef managers, scientists and other stakeholders, to best support reef recovery after a disturbance. The overall aim of this management framework is to catalyse reef recovery, to minimize recovery times, and to limit the need for ongoing management interventions into the future. Our framework includes two main stages: first, a prioritization method for assessment following a large-scale disturbance, which is based on a reef's social-ecological values, and on a classification of the likelihood of recovery or succession resulting in degraded, novel, hybrid or historical states. Second, a flow chart to assist with determining management actions for highly valued reefs. Potential actions are chosen based on the ecological attributes of the disturbed reef, defined during ecological assessments. Depending on the context, management actions may include (1) substrata rehabilitation actions to facilitate natural coral recruitment, (2) repopulating actions using active restoration techniques, (3) resilience-based management actions and (4) monitoring coral recruitment and growth to assess the effectiveness of management interventions. We illustrate the proposed decision framework with a case study of typhoon-damaged eastern outer reefs in Palau, Micronesia. The decisions made following this framework lead to the conclusion that some reefs may not return to their historical state for many decades. However, if motivation and funds are available, new management approaches can be explored to assist coral reefs at valued locations to return to a functional state providing key ecosystem services.

1. Introduction

Disturbances of coral reef systems are increasing in frequency and intensity due to global climate change, eroding reef recovery potential (Ainsworth et al., 2016; Cheal et al., 2017; Cinner et al., 2009; Graham et al., 2011; Hoegh-Guldberg et al., 2007; Ortiz et al., 2018). The rate of climate change impacts may not leave enough time for coral reefs to recover in between disturbance events (Hoegh-Guldberg et al., 2007; Hughes et al., 2018; Osborne et al., 2017; Pandolfi et al., 2011). Although refugia exist where coral reefs have demonstrated adaptation to extreme conditions (Palumbi et al., 2014; van Woesik et al., 2012), such refugia are not widespread. Following large-scale disturbances, such as mass coral bleaching or cyclonic events, it commonly takes 8–12 years, even in shallow coral reef slope communities (<15 m), to recover to a coral-dominated state (Adjeroud et al., 2009; Baker et al., 2008; Connell, 1997; Gilmour et al., 2013; Gouezo et al., 2019; Johns et al., 2014). While reducing greenhouse gas emissions on a global scale is key to the persistence of coral reefs in the future, local coral reef

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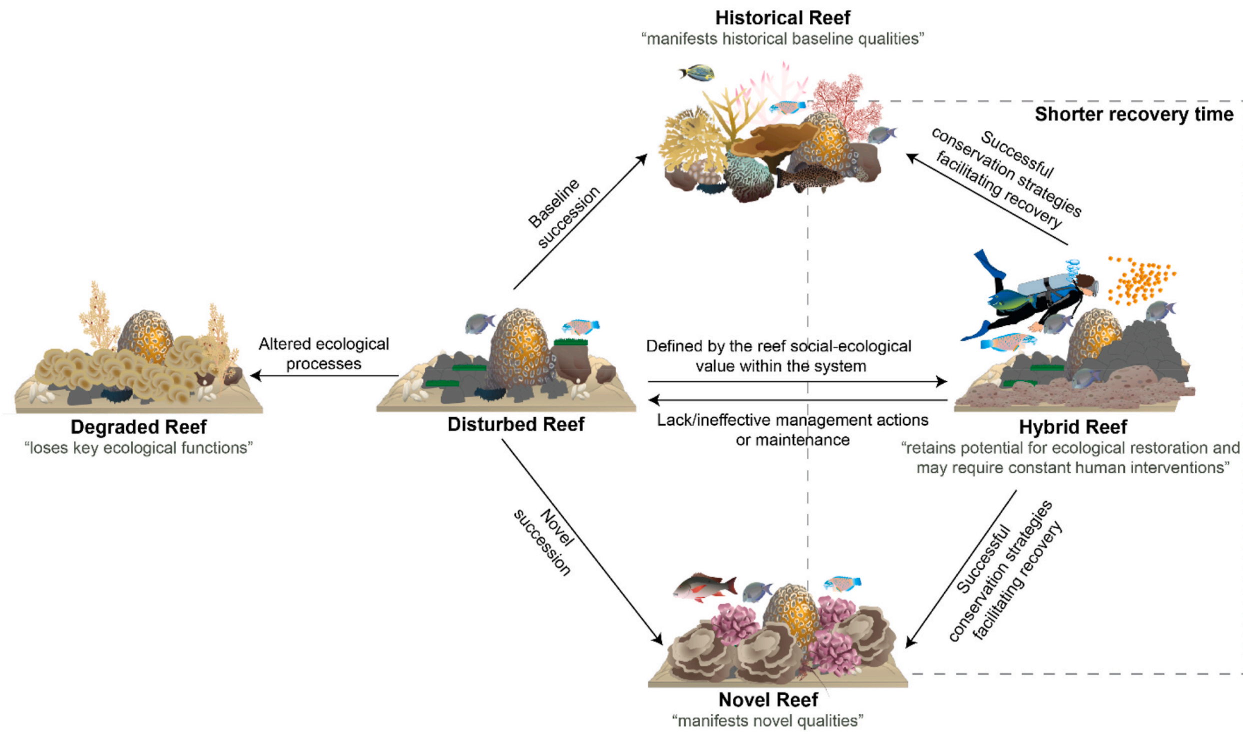

Fig. 1. Conceptual diagram highlighting the differences in reef type classification: historical, disturbed, degraded, hybrid and novel reef in the context of managing reef to optimize recovery.

management strategies must focus on optimizing the recovery potential of coral reefs and the conditions in which they thrive.

Resilience-based management that includes controlling land-based pollution, implementing marine protected areas (MPAs), catch/size limits, quotas, and fisheries closures (Anthony et al., 2020; Bellwood et al., 2019; Fabricius, 2005) remains a key conservation strategy that supports reefs and dependent communities (Mcleod et al., 2019). However, the ability of such approaches to sufficiently boost coral resilience in response to severe global disturbances is contentious (e.g. Bruno et al., 2018; Donovan et al., 2021). Following a disturbance, management actions should also be aimed at shortening both the lag phase and the growth phase during early community recovery (Gouezo et al, 2019, 2020,; Ortiz et al., 2018), using a combination of resilience-based and restoration management approaches. The length of the lag phase differs between reefs and coral species due to larval supply and coral recruitment processes occurring at various rates along environmental gradients (Doropoulos et al., 2017; Gouezo et al., 2020; Ortiz et al., 2018; Wolfe et al., 2020). Similarly, the length of the recovery phase varies widely depending on location and coral species (e.g. Anderson et al., 2017). Therefore, the biophysical drivers of recovery at specific reefs need identification and integration into conservation and restoration strategies.

Processes that facilitate coral recruitment and recovery after disturbances have been investigated in numerous studies (e.g. Doropoulos et al., 2016; Gilmour et al., 2013; Gouezo et al., 2019; Graham et al., 2015, 2011). Asexual recovery, through fragmentation, tissue regeneration and/or re-growth of remnant colonies, typically follow mild disturbances that do not alter the environment (Connell et al., 1997; Diaz-Pulido et al., 2009; Gilmour et al., 2013; Roff et al., 2014; Wallace, 1985). When disturbances are severe, removing most live corals (Table S1) and altering the surrounding environment, the length of the lag phase of recovery will depend predominantly on sexual reproduction followed by recruitment of corals. Recruitment that results from sexual reproduction is influenced by biophysical factors operating on the three phases of larval supply, larval settlement, and post-settlement survival and growth for coral populations (Harrison and Wallace, 1990). Biophysical drivers can facilitate (such as high herbivory levels) or inhibit (such as high coverage of rubble or fleshy algae) any of the coral recruitment phases individually or in combination (Dajka et al., 2019; Doropoulos et al, 2016, 2017, 2016; Gouezo et al., 2020) (e.g. Figure S3-S5). Conservation strategies should therefore aim to promote those biophysical drivers where possible.

Several conservation and restoration strategies exist to assist natural recovery of coral reefs, including indirect (e.g. spatial management, catchment rehabilitation) or direct (e.g., adding larvae, coral gardening, engineering substrata, supporting selective adaptation) management actions (Anthony, 2016; Hein et al., 2020; Van Oppen et al., 2017). However, what is often missing from management action plans is a prioritization and localized strategy based on both the social and ecological context of the reef system that has been damaged by a disturbance. By identifying the constraints to recovery in the social-ecological context of the reef system and addressing them through conservation management actions, there is a higher likelihood for disturbed reefs to regain their key ecosystem functions (Brandl et al., 2019).

Coral reefs are considered as social-ecological systems due to their equally important social and ecological characteristics; both of which need integration during conservation management (Cinner, 2014; Cinner et al., 2009). Economic benefits occur through fisheries (Newton et al., 2007) and tourism (Spalding et al., 2017) for example, and social-cultural values are supported by cultural and spiritual traditions or artistic inspiration (Moberg and Folke, 1999). Integrating customary management into modern marine conservation has resulted in management successes including cultural respect and community engagement in island nations (Clements et al., 2012; Hamilton et al., 2011). For example, active coral reef restoration actions involving communities has provided strong social-cultural benefits such as education, awareness or stewardship (Hein et al., 2017). Therefore, a quantification of the existing social, cultural and economic values of different reefs needs to be integrated with the quantification of their ecological characteristics to help managers decide on where and how to act and under what strategy (Shaver et al., 2020).

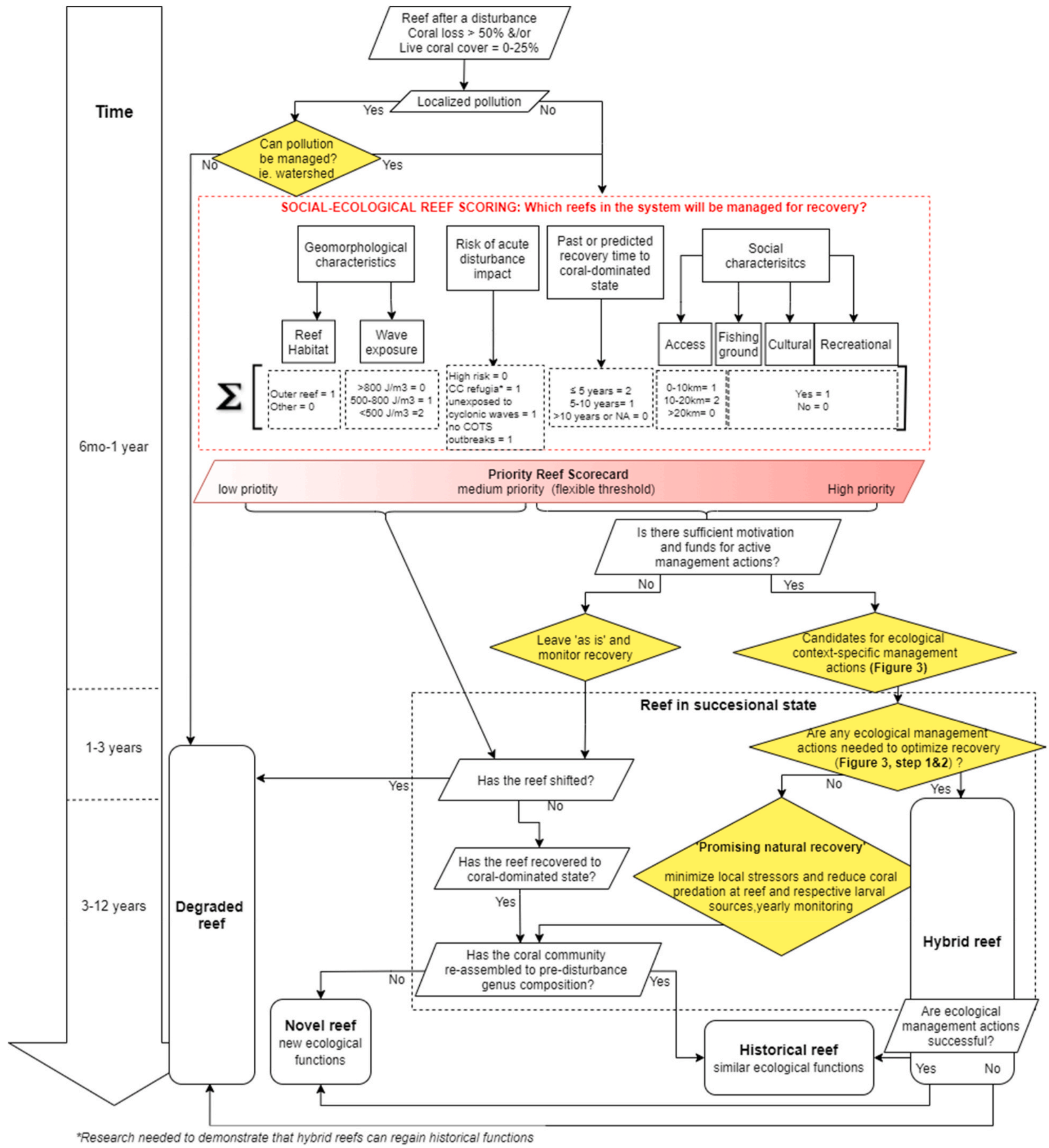

Fig. 2. Decision tree applying the novel/hybrid/historical ecosystem concept as a prioritization method to classify reefs after a large-scale disturbance leading to 0–25% coral cover and/or live coral loss of ≥50% (Table S1). Details on social-ecological scoring rationales are provided in Table 1. Shapes follow the standardized symbols for decision flow charts: parallelogram = data needed, rectangle = process 1, rounded rectangle = process 2, yellow diamond = decision required for management actions during the prioritization phase. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

In this discussion paper, while synthesizing advances in coral reef recovery research and applications of these new insights to conservation management, we provide a framework to guide the decision-making capacity of scientists and managers to best support the recovery of reefs following a disturbance. The overarching goal of this framework is to catalyse the recovery of coral reefs and reduce the need for interventions through time. The main objectives are to: (1) integrate reefs' social-ecological values within the 'novel/hybrid ecosystem' concept to spatially prioritize management actions following a disturbance; (2) contextualize management actions at prioritized reefs based on available ecological knowledge; and, (3) illustrate this framework with a case study using the eastern outer reefs of Palau. We conclude by discussing important knowledge gaps in coral recovery that would benefit from further research and suggest improvements in coral reef monitoring programs.

2. Valuing reefs to spatially prioritize management actions

The prioritization of spatial conservation management based on biodiversity attributes and social values has been studied extensively for

Table 1
Social-ecological variables and their rational determined to quantify the answer to the question: "Which reefs in the system will be managed for optimized recovery?". The rationale may be specific to Palauan reefs and therefore would need to be adapted to the social-ecological context of other systems.

Social-ecological reef scoring variables	Rationale for Pacific island reefs system such as Palau
Ecological and environmental variables	
Reef habitat	Outer reef slopes are favored for their increased productivity and fisheries benefits (Harborne et al., 2018). This can be defined using coral reef habitat map (e.g. NOAA, 2014)
Exposure to wave energy	Highly exposed reefs are difficult to access and overall slower to recover. This can be calculated using GIS techniques (e.g. Houk et al., 2014)
Additional risk of future acute disturbances as determined by past exposure	Reefs with low past bleaching prevalence, termed 'climate change refugia', and reefs not orientated to past typhoon waves are favored (e.g. Gouezo et al., 2015; van Woesik et al., 2012)
Recovery pace after the 1998 global mass bleaching event	Reefs with fast recovery pace are favored (e.g. Golbuu et al., 2007; Gouezo et al., 2019)
Socioeconomic variables	
Community access to the reef	Reefs favored in a non-linear manner. Often, nearshore reefs are either already overexploited by communities or impacted by land pollution, and therefore investment into travelling to reefs a bit further away (10–20 km) but up to a limit (>20 km) due to fuel costs and weather conditions. This can be calculated as the distance from the reef to the nearest human community.
Fishing grounds	Quantified through key informants' interviews (e.g. Table S3) as reefs that are frequently visited and important to local fishers
Cultural	Quantified through key informants' interviews as reefs that have a specific cultural importance such as historical or spiritual values
Recreational	Reefs that are highly visited by locals and/or tourists for recreational activities such diving, snorkeling and family gatherings

the past two decades (Foley et al., 2010; Klein et al., 2010; Leslie, 2005), as exemplified by the development and application of the software 'Marxan' (Ball et al., 2009; Possingham et al., 2000). Since then, other attributes have been incorporated within the prioritization of conservation measures such as climate change projections (Jones et al., 2016), connectivity (Beger et al., 2010), and land-sea connections (Brown et al., 2019). Here, we develop a framework inspired by the degraded/novel/hybrid/historical ecosystem concept (Hobbs et al., 2013), recently applied to marine systems (Schläppy and Hobbs, 2019), to assist decision-makers on where and how to prioritize conservation resources on coral reefs following disturbances.

When a reef is disturbed and no management is undertaken, it may take one of three different trajectories if given enough time until the next disturbance: (1) be stuck in or further deteriorate into a degraded state if ecological processes are chronically altered, (2) recover to its historical state, or (3) recover to a novel state (Fig. 1). Direct (e.g., overfishing) and indirect (e.g., global climate change) human impacts have re-shaped ecosystems, leaving only 13% of ocean areas truly "wild" (Jones et al., 2018), and leading to the concept of 'novel' ecosystems (Backstrom et al., 2018; Hobbs, 2016; Hobbs et al., 2013). Novel ecosystems are defined as "a system of abiotic, biotic and social components (and their interactions) that by virtue of human influence, differ from those that prevailed historically, having a tendency to self-organize and manifest novel qualities without intensive human management" (Hobbs et al., 2013). Examples of novel coral reefs include some reefs in Mo'orea, French Polynesia, which recovered to their pre-disturbance cover but are now dominated by Pocilloporidae corals that have replaced *Acropora* spp. as the previously dominant coral group (Adjeroud et al., 2018; Holbrook et al., 2018). Many Caribbean reefs have shifted from *Acropora* spp. and *Orbicella* spp. dominated communities to *Agaricia* spp. and *Porites* spp. dominated communities (Green et al., 2008) that are now more resistant to disease outbreaks (Yakob and Mumby, 2011). Such novel reefs have altered ecological functions compared to their historical predecessors, even though they remain calcifying, coral-dominated reefs (Graham et al., 2014). Novel reefs contrast from (1) historical reefs that have returned to historical baseline (Hobbs et al., 2006), (2) degraded reefs that have lost their key historical ecological functions, resulting in the loss of ecosystems goods and services (Hobbs, 2016), or (3) from disturbed reefs that are in early successional states and could remain in such states for extended periods of time (e.g. low coral cover communities (Edmunds, 2018)) (Fig. 1).

When a reef is disturbed yet retains sufficient social-ecological values, it becomes suitable for context-specific management actions (Figs. 1 and 2). This conceptually shifts the disturbed reefs into a transient 'hybrid' stage (Schläppy and Hobbs, 2019) (Fig. 1). Hybrid reefs are therefore selected by humans as potential candidates for management actions. These actions will accelerate the recovery of the reef to transition into a novel or historical state once key ecological functions return. However, if management fails, it will remain altered. While hybrid reefs are likely to be transient, they may also require prolonged human interventions and therefore remain in a hybrid state for some time (Schläppy and Hobbs, 2019). It is important to identify hybrid ecosystem 'candidates' using a prioritization process quickly after a disturbance, so that resources can be optimally allocated. Such decisions will inherently lead to the acceptance that some ecosystems may never return to historical states but can remain functional and continue to provide ecosystem services. To help with the decision-making process, we present a scoring system based on social, economic and ecological characteristics to help value reefs following a disturbance (Fig. 2).

Following the decision tree presented in Fig. 2, reefs that are exposed to unmanageable and visibly damaging levels of pollution after a large disturbance would be generally be classified as 'degraded reefs' because of the overwhelming evidence that high levels of nutrients and sedimentation negatively affect coral recruitment, reef recovery and resilience (Fabricius, 2005; Humanes et al., 2016; MacNeil et al., 2019; Ortiz et al., 2018; Wakwella et al., 2020). At reef locations where there is little pollution or if pollution were to be managed, disturbed reefs would be scored according to their social-ecological values defined by four environmental and four socioeconomic variables (Table 1). These characteristics were defined as key determinants to quantify the answer to the question: "Which reefs in the system will be managed for optimized recovery?". These variables are based on previous research for Pacific island reef systems and selected in accordance with socioeconomic researchers engaged in monitoring activities by the Palau International Coral Reef Center (e.g. Marino et al., 2020). They may be adapted depending on specific regional system properties (i.e., they are context-specific). The total score of all disturbed reefs are then calculated by summing the integers from each scoring category (Fig. 2).

For example, a reef with the lowest value would include the following characteristics: polluted, high wave exposure, frequently disturbed historically, recovery rate >10 years, remote, and socially unimportant to the local community. A reef with the highest score would include: non-polluted, outer reef, low to medium level of wave energy, not exposed to severe typhoon waves, low bleaching prevalence, high social-cultural-economic importance to the community, and fast recovery or predicted recovery (5–10 years). Reefs with the highest scores are more likely to be selected for active interventions that promote reef recovery. In contrast, reefs with a medium score threshold will depend on the willingness to intervene based on the availability of people, funds and other resources.

Reefs with low priority scores would not be highly prioritized for regular monitoring if monitoring resources are limited. Without

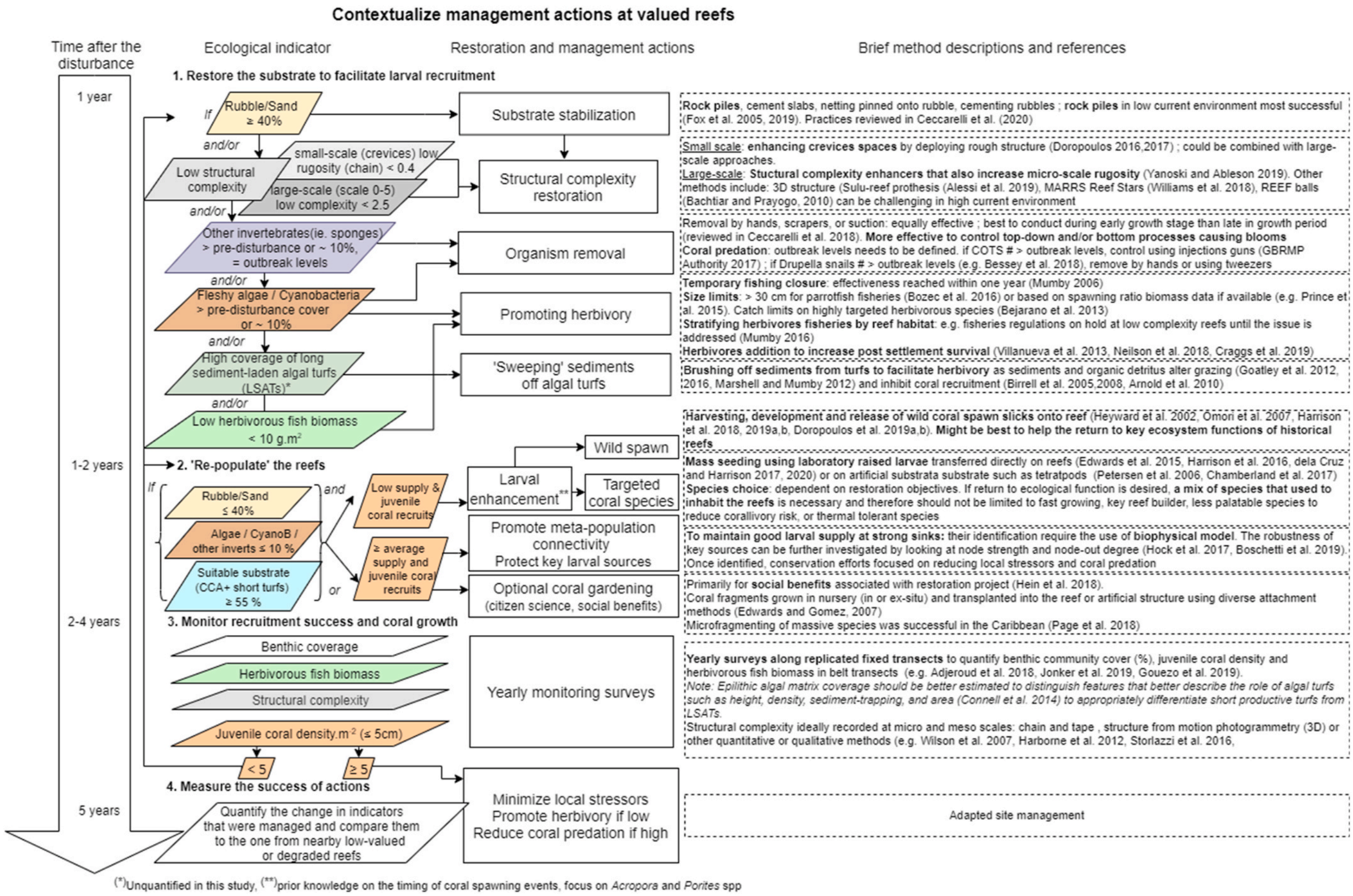

Fig. 3. Flow chart detailing steps to take after a disturbance at prioritized reefs, where management actions can be contextualized based on the ecological features of the reef. Shapes follow the standardized symbols for decision flow charts: parallelogram = data needed, rectangle = process. Threshold values were extracted from Gouezo et al. (2019, 2020) (Figure S3-S5) for the reef system of Palau; these values may differ for other reef systems.

intervention, these reefs have the likelihood to remain or become degraded reefs (i.e. phase shifted), novel reefs (i.e. coral-dominated with different community composition) or historical reefs (i.e. coral-dominated state with similar community composition) over prolonged periods of time in the absence of further disturbance(s).

In a scenario where funds, people and other resources are available, reefs with medium to high reef scores would become hybrid reefs if active conservation interventions are needed at the site (Van Oppen et al., 2017). Management actions at these reefs will be contextualized based on ecological knowledge and data collected at the sites following the disturbance (see Section 3). If medium to high valued reefs are expected to have a positive natural recovery trajectory, they would not require any management interventions (see Section 3). In this scenario, conservation actions should focus on minimizing local stressors and reducing coral predation (e.g., from crown-of-thorns starfish) at respective larval sources (if known), as well as conducting regular monitoring. Conversely, if willingness to intervene and resources are not available, their recovery will not be optimized and these reefs will remain in transient states for a minimum of five years up to multiple decades (Connell, 1997; Edmunds, 2018; Tanner, 2017). Annual monitoring at valued reefs will determine trajectories and should focus on collecting data on key ecological indicators (e.g. Lam et al., 2017) (further described in Section 3). Regular assessments of larval supply and/or settlement are also necessary for the first two years if information is not already available on the evenness and distribution of larval sinks (Gouezo et al., 2021). Research is still required to demonstrate if hybrid reefs can regain historical ecological functions after interventions.

3. Contextualizing management actions at valued reefs based on ecological knowledge

Once reefs have been classified and hybrid reef candidates selected, management goals can be contextualized depending on the ecological attributes of the reef, following the flow chart in Fig. 3 and detailed in the following subsections. These management goals should first focus on assessing, and if necessary, rehabilitating the reef substrata to facilitate natural larval recruitment to enhance settlement and reduce post-settlement mortality; second, determining whether artificial repopulation of the reef is needed; and lastly, monitoring the recruitment success, growth and survival of newly colonized corals (Fig. 3).

3.1. Restoring the substrata to facilitate larval settlement

If coral larvae are naturally supplied to reefs, properties of the reef substrata are the first determinants for coral settlement success. Loose substrate made of coral rubble and sand can be abundant at some reefs especially following storms, inhibiting coral larval settlement and intensifying coral post-settlement mortality (Chong-Seng et al., 2014; Fox et al., 2003; Fulton et al., 2019; Kenyon et al., 2020; Yadav et al., 2016). Rock piles, cement slabs or stabilizing mesh placed onto rubble fields may locally speed up the stabilization phase of rubble fields (reviewed in Ceccarelli et al., 2020) in low to medium current environments (Fox et al, 2005, 2019), as rubble consolidation is a lengthy process (Rasser and Riegl, 2002). This approach would also increase both micro- (i.e. crevices) and meso-scale complexity (as shown by Yanovski and Abelson (2019) with rough rock piles) and could

Table 2
Studies showing juvenile coral (≤5 cm) density per m^2 that led to a subsequent increase in coral coverage 1–3 years later during natural recovery.

Locations	Juvenile coral density per m^2 threshold	Taxa	References
Palau	1.5	*Acropora*	Gouezo et al. (2019)
Palau eastern reefs	>5	All	Gouezo et al. (2020)
Seychelles	6.2	All	Graham et al. (2015)
Moorea	3–12	All	Adjeroud et al. (2018)
Moorea	5	*Pocillopora*	Bramanti and Edmunds (2016)
Okinawa	2–4	*Acropora & Pocillopora*	Edmunds et al. (2015)
East Australia (Great Barrier Reef)	>1.5	*Acropora*	Doropoulos et al. (2015)
East Australia (Great Barrier Reef)	>8	All	Connell et al. (1997)
West Australia (offshore atoll)	1.2	*Acropora*	Gilmour et al. (2013)

positively influence coral recruitment (Doropoulos et al, 2016, 2017, 2016; Edmunds et al., 2014; Suzuki et al., 2011). Other large structures deployed to rehabilitate meso-scale complexity have had some reported benefits such as 'Sulu-reef prothesis' (e.g. Alessi et al., 2019), REEF balls (e.g. Bachtiar and Prayogo, 2010), or hexagonal-shaped structures (MARSS Reef Stars) (Williams et al., 2019), but these approaches are expensive and will likely remain restricted to small-scale interventions. Further detailed research is needed to properly evaluate their usefulness in local reef restoration. With present designs, these types of structures must be used in combination with coral gardening approaches; however, they could be redesigned with micro-structure rugosity to promote natural or enhanced coral recruitment (settlement and post-settlement growth and survival).

Competitors for space other than corals (predominantly algae, but also corallimorpharians, soft corals, sponges and other invertebrates) can quickly establish dominance on open substrata following disturbance (Birrell et al., 2008; Doropoulos et al., 2014; McCook et al., 2001; Roff et al., 2015). Organism removal actions can be implemented if there are sufficient people and resources available, with various approaches reviewed in Ceccarelli et al. (2018). However, it is best to control the bottom-up and/or top-down processes causing the over-abundance of these organisms when possible, as addressing the causes will have longer-lasting effects, improve the resilience of the reef, and are more effective at larger scales. A combined approach of (1) direct removal of most non-habitat-forming macroalgae, (2) the addition of grazers and (3) control of nutrients, while ambitious, may be essential to help restore ecological balance at a faster pace.

In the case of macroalgal phase shifts, managing herbivorous fisheries via fishing closures or catch size limits have been successful (Bozec et al., 2016; Mumby, 2006; Mumby et al., 2021), except in circumstances where there is too much sedimentation on the substrate that prevents grazing (Goatley et al., 2016; Tebbett et al., 2017) and/or coral recruitment (Wakwella et al., 2020). High coverage of relatively tall, sediment-laden algal turf can inhibit coral recruitment because of their ability to trap sediments (Arnold et al., 2010; Birrell et al, 2005, 2008) and prevent grazing (Goatley and Bellwood, 2010; Marshell and Mumby, 2012). Therefore, brushing off the sediments from substrata and algal turfs should be tested to determine whether it may help facilitate grazing from herbivorous fish and coral recruitment (Speare et al., 2019). The addition of micro-herbivores such as the gastropod *Trochus niloticus* (Villanueva et al., 2013) or the sea urchin *Mesilipilia globulus* (Craggs et al., 2019) can increase the survivorship of early-stage corals in *ex situ* settings and could be tested to gauge the effects on post-settlement survival *in situ* on the reef (Omori and Iwao, 2014). To our knowledge, no studies have tested the effects of adding herbivorous fish from aquaculture nurseries onto degraded coral reefs, but manual algal removal followed by the addition of nursery-raised urchins onto Hawaiian patch reefs showed a 85% reduction of macroalgae cover (Neilson et al., 2018).

Coral predation may occur above normal rates because of predator population outbreaks, requiring management actions to control and limit predator densities. The two major coral predators that often occur at or above outbreak densities are *Acanthaster* spp. and *Drupella* snail spp. (Bessey et al., 2018; Fabricius et al., 2010; Moran and De'Ath, 1992). Once outbreak densities are defined for the system, eradication control actions could be conducted such as killing *Acanthaster* spp. using injections of lethal bile salts or vinegar (Boström-Einarsson and Rivera-Posada, 2016), or removing *Drupella* snails by hand or using tweezers around corals to carefully extract them. These approaches are time consuming, costly and likely to remain small-scale controls, unless sufficient resources are allocated such as for the COTS control program on the Great Barrier Reef (e.g. GBRMPA, 2020a).

3.2. Re-populating the reef

Where reef substrata are suitable for larval settlement and larval supply is low, enhanced larval supply restoration actions can help speed up coral reef recovery (Harrison et al. 2019a; dela Cruz and Harrison, 2020; 2017). Several larval restoration methods have been developed, including the harvesting of wild spawn and release of larvae at different scales (Doropoulos et al., 2019a, 2019b; Harrison, 2018; Harrison et al., 2019a, 2019b; Heyward et al., 2002), to mass seeding of laboratory-raised larvae directly to the reefs (dela Cruz and Harrison, 2017; 2020; Edwards et al., 2015), or to artificial substrata, which are then deployed onto reefs (Chamberland et al., 2017; Petersen et al., 2006).

For mass larval enhancement, the choice of species should correspond with local priorities to assist natural recovery. It is recommended to focus on key species that previously inhabited the reef, i.e., assist the succession towards 'historical reefs'. Hence efforts should not be limited to fast growing, less palatable, or thermally/*Acanthaster*/wave-tolerant species, although the latter would increase chances of resisting future disturbances. Techniques capturing wild spawn slicks with their broad genetic diversity may be better suited to help coral reefs regain their key ecological functions and maintain genotypic diversity within species (Harrison et al., 2019a, 2019b; Doropoulos et al, 2019a, 2019b; Heyward et al., 2002; Rinkevich, 1995).

Where substrata are suitable for larval settlement and larval supply is average or high, resources should be allocated to protecting the key larval sources to the disturbed reefs (sinks). Protecting highly connected sources will help maintain and/or promote meta-population connectivity (Doropoulos and Babcock, 2018; Hock et al., 2017; Jones et al., 2009), but this requires biophysical modelling (e.g. Bode et al., 2006; Figueira, 2009; Hock et al., 2017). The robustness of the connectivity of sources to sinks can be further investigated based on connectivity node strengths from modelled dispersal events over a few years (Boschetti et al., 2020; Feng et al., 2016; Gouezo et al., 2021; Hock et al, 2017, 2019), and from monitoring coral larval settlement and recruitment patterns on target reef areas (Gouezo et al., 2020).

Because of the positive social benefits that can arise from coral restoration projects (Bayraktarov et al., 2020; Hein et al., 2019; Williams et al., 2019), initial coral restoration projects could be implemented at small scales to educate and raise awareness within communities. These might involve establishing nurseries in which naturally fragmented corals are given time to grow before being attached to the reef, or culturing coral larvae for settlement directly on reefs (dela Cruz and Harrison, 2020; 2017) or pre-settlement on devices

Table 3
Scoring of Palauan eastern outer reef sites to prioritize management efforts following large-scale disturbance following our decision tree flow diagram (Fig. 2). The locations of the reefs are shown in Fig. 4, S1. [(1)]Gouezo et al., (2020), [(2)]Golbuu et al. (2011), [(3)]NOAA habitat map (NOAA, 2014), [(4)]based on wave exposure GIS tool providing 10 years' average wave energy (Table S2), [(5)]Marsh and Tsuda (1973),[(6)]van Woesik et al. (2012), [(7)]distance calculated from the reef to nearest town, village or boat ramp, [(8)]based on key fishermen informants interview (Table S3), [(9)]popular dive or snorkelling sites locations.

Scoring categories		Study Sites 1	2	3	4	5	6	7	8	9
Disturbance impact	Live coral cover (%) after typhoons[(1)], <25% (Y/N)	4, Y	3, Y	1,Y	4,Y	1.Y	5,Y	1,Y	1,Y	0.2,Y
Anthropogenic	Pollution[(2)] (Y/N)	N	N	N	N	N	N	N	N	N
Geomorphological	Reef habitat[(3)]	2	2	2	2	2	2	2	2	2
	Wave exposure[(4)]	0	0	0	1	0	1	2	0	2
Low acute disturbance	Unexposed to typhoon waves[(1)]	0	0	0	0	0	0	0	0	0
Risks	No historical *Acanthaster* outbreak[(5)]	1	1	1	1	1	1	0	0	1
	Climate change refugia[(6)]	0	0	0	0	0	0	1	1	0
Social	Access[(7)]	0	0	2	2	2	1	2	1	1
	Fishing ground[(8)]	1	1	0	0	1	1	0	0	1
	Recreational[(9)]	0	0	0	0	0	1	1	0	1
	Cultural[(8)]	0	0	0	1	0	0	0	0	0
Past recovery time in years (not available for all sites)		N/A	N/A	2	2	0	1	0	N/A	1
Priority score (sum of ratings excl. past recovery score)		4	4	**5**	**7**	6	**7**	8	4	8
Hybrid reef candidate? (Y/N)		N	N	Y	Y	Y	Y	Y	N	Y

Table 4
Mean values for each ecological indicator recorded after the disturbance at studied valued reefs to be used for context-specific actions to restore the substrata for larval recruitment (1) and/or to repopulate the reefs (2). Monitoring data and threshold values (in brackets) are color coded to compare values against the thresholds identified by Gouezo et al. (2020, 2019) (green: better, orange: near, red worse than the threshold, and black if threshold values are unknown or unclear) (Figure S3-S5). [(1)]Herbivorous fish analysis can be found in Supplementary Information.*Turf algae data do not provide accurate resolution for the coverage of long sediment-laden algal turfs versus short productive turfs. **Localized larval pulses that likely occurred in 2014 (a year not studied for larval settlement in Gouezo et al., 2021) or the retention effect not detected at the resolution of the biophysical model.

	Ecological indicators (threshold values from Gouezo et al. (2020, 2019))	Valued Study Reefs **3**	**4**	**5**	**6**	**7**	**9**
1	Rubble/sand (< 40%)	4.6	**41.4**	9.3	**74.4**	**69.4**	23.3
	Macroalgae (< 10%)	0	4.2	0.2	0	0	0.7
	Turf algae* (? %)	86.2	42.6	76.6	15.7	22.3	22.8
	CCA (3 – 10%)	2.9	9.3	7.6	**2.5**	**0**	3.8
	Other benthic invertebrates (< 10%)	0.3	1.3	0	0.8	0.8	0.6
	Habitat complexity (large-scale) (> 2.5)	2.75	**2.25**	3	3	**1.5**	3
	Rugosity (> 0.4)	**0.39**	0.54	0.55	**0.34**	**0.21**	0.45
	Targeted herbivorous fish (> 8 $g.m^{-2(1)}$)	**3.69**	**0.48**	**3.46**	**3.95**	**3.3**	**4.52**
2	Suitable substrata (≥ 55%)	91.9	52.1	84.4	**18.5**	**28.9**	72.6
	Larval supply/settlement (i.e., modelled larval retention and settlement rate on tiles)	**below average**	**below average**	average	average	Above average	**below average****
	Juvenile coral density per m^2 two years post-disturbance (> 5 m^{-2})	**4.2**	**0.3**	9.1	8.7	**1.7**	19.1

that are subsequently outplanted onto degraded reefs (Chamberland et al., 2017). Additionally, micro-fragmenting massive coral species has been used in the Caribbean where predation was low (Page et al., 2018).

3.3. Recruitment success and coral growth monitoring

Regular yearly ecological monitoring before, during, and following restoration actions are needed to assess successes or failures. Monitoring benthic coverage, herbivory, structural complexity, and juvenile coral densities are amongst the top ecological indicators to focus on during early reef recovery (dela Cruz and Harrison, 2020, 2017; Flower et al., 2017; Graham et al., 2015, 2011). Previous literature suggests a minimum threshold of juvenile coral densities of >5 individuals m^{-2} is needed for subsequent recovery in live cover coral coverage 1–3 years later (Table 2). If juvenile densities are equal to or above that threshold, management of the site should focus on maintaining good herbivory biomass levels (e.g., >10 $g.m^{-2}$ on Pacific reefs (this study, Holbrook et al., 2016)), reducing coral predation, and controlling other stressors (e.g. fishing, anchoring). If juvenile densities are well below that threshold, re-assessment and interventions at the site will be needed (return to Step 1, Fig. 2).

3.4. Measuring the success of management actions

Research and monitoring at valued reefs over at least the timeframe needed for corals to reach sexual reproductive size (dela Cruz and Harrison, 2017), but ideally 10–15 years to capture full recovery, is needed to assess the long-term success or failure of management actions (Abelson, 2006; Hein et al., 2020). This requires a set of clearly defined ecological indicators that will be used to evaluate specific objectives and outcomes from management interventions. Monitoring over five years has occurred in less than 20% of coral restoration projects reviewed in Hein et al. (2017), limiting our understanding of restoration success (Boström-Einarsson et al., 2020; Hein et al., 2020). The regular monitoring of ecological indicators defined in Step 3 (Fig. 2), conducted every year ideally, would allow (1) the quantification of changes through time, and (2) characterisation of the effectiveness of management actions. For (2), ecological indicators need to be monitored at a nearby low-valued or degraded reefs that share similar environmental characteristics (i.e., paired control). This type of research will help improve our understanding of novel coral reefs and their associated ecosystem functions and services (Graham et al., 2014), as well as the assessment of different management approaches. Relevant findings can then be integrated to inform the current decision-making processes to develop and implement policies on active interventions on reefs within a managed system (e.g. GBRMPA, 2020b).

4. Case study: the eastern outer reefs of Palau

4.1. Brief context

We focused on nine reef sites located along the eastern outer reefs of Palau (Figure S1) that were extensively damaged by two consecutive super typhoons in 2012 and 2013 (Gouezo et al., 2015) and where recovery was studied (Gouezo et al, 2019, 2020, 2021). Several other studies helped defined social-ecological attributes of reefs and are referred to in Table 3. With this data-rich example, we aim to demonstrate the feasibility of our decision-making framework for prioritizing and contextualizing management actions following a large-scale disturbance. We focus on reefs located at 10 m depth.

The super-typhoons reduced average live coral cover from ~35% to 6% on these reefs, severely reducing structural complexity and

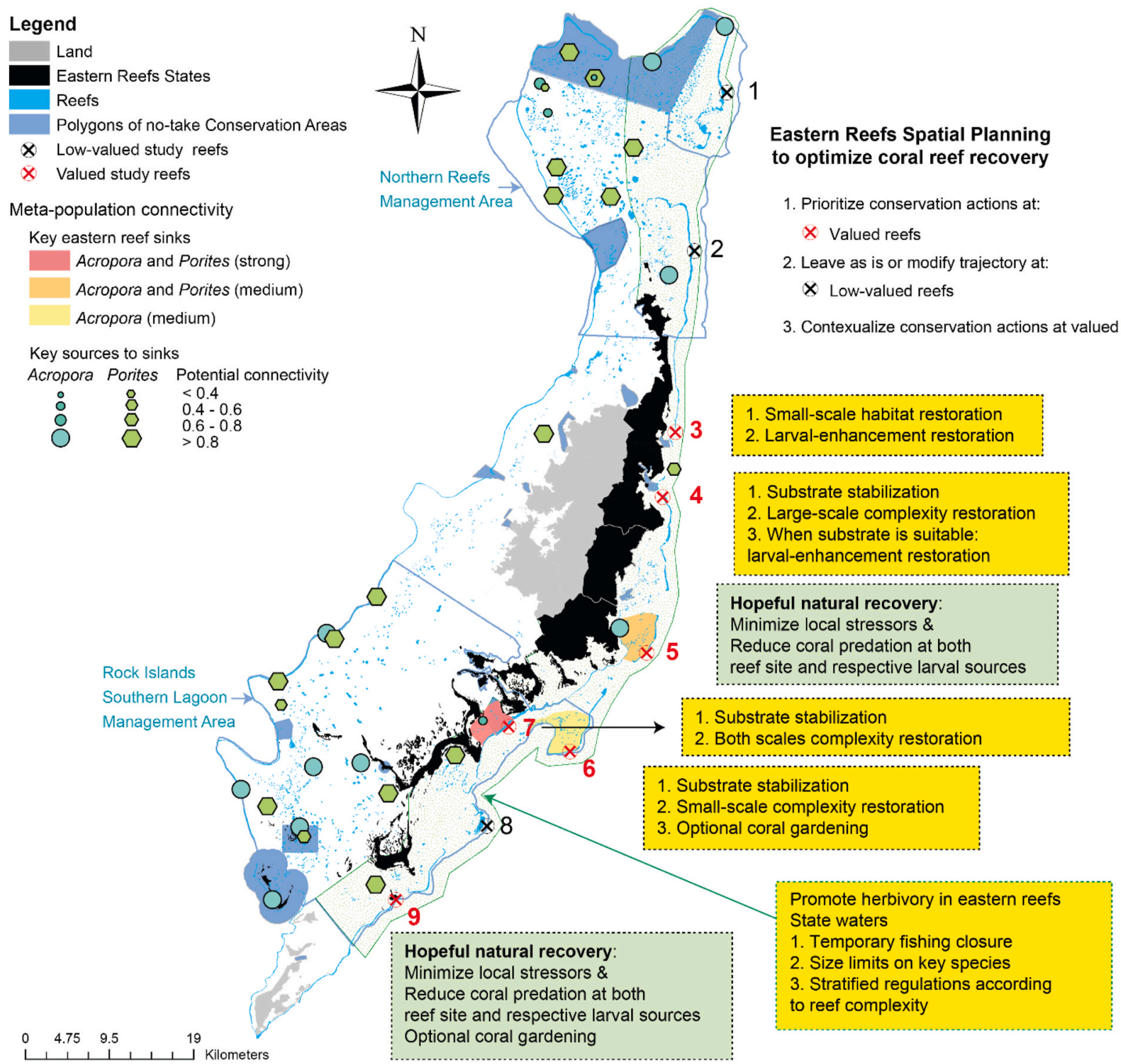

Fig. 4. Map displaying the conservation spatial planning on the eastern reefs to optimize coral reef recovery following intense typhoon disturbances.

increasing rubble and sand cover (Gouezo et al., 2015) (Figure S1, S2). Monitoring data show that five years following the typhoons, live coral cover within the eastern outer reefs remained low (6.4%) and has not increased for the past five to six years, i.e., the reefs remain in the 'lag phase' of recovery even though the coral community is slowly re-assembling by increasing diversity (Figure S1). It is expected that their recovery following such destructive disturbances will take longer than following the 1998-bleaching event (i.e. 9-12 years), if no management actions are taken. Changes in the substrata properties of reefs (Gouezo et al., 2020), in combination with overall low coral larval supply (Gouezo et al., 2020, 2021), are likely driving their relatively long lag phases of recovery.

4.2. Reef valuation to prioritize management actions

Using the decision tree (Fig. 2) and based on available social-ecological knowledge of the system (Table 3), we identified reefs with the greatest social-ecological value within the eastern outer reef system. Typhoon impacts were high along the coast, but local pollution is low and most sites are located far from terrestrial runoff and major watersheds (Golbuu et al., 2011). Therefore, all reefs were in unpolluted environments and were scored accordingly (Table 3). Sites 9, 7, and 4 had the highest values because of their medium wave exposure, social characteristics and/or fast recovery pace from 1998 mass bleaching impacts; while Sites 1, 2, and 8 had the lowest values because of exposure to high wave energy, remoteness, and low social value. Past recovery data were not available for sites 1, 2, 7, and 8 and therefore, we excluded this category in the final sum of ratings (Table 3). For this assessment, we assume that funds, people and other resources are available to implement management actions at the reefs that scored >5, leading to selecting 6 reefs out of 9 as candidates to potentially apply management actions.

4.3. Contextualize management actions at valued reefs

Reef assessments of valued reefs were conducted in 2016, two years after the two typhoons, using the methodologies described in Gouezo et al. (2020, 2019). The average indicator values among the five transects are given for each reef at 10 m depth (Table 4). The contextualization of management actions at each site was conducted following the diagram of Fig. 3. All management actions based on data from Table 4 are summarized in Fig. 4.

The reef assessment data showed considerable coverage of rubble and sand at sites 4, 6 and 7 (Table 4). Two of these sites also had low

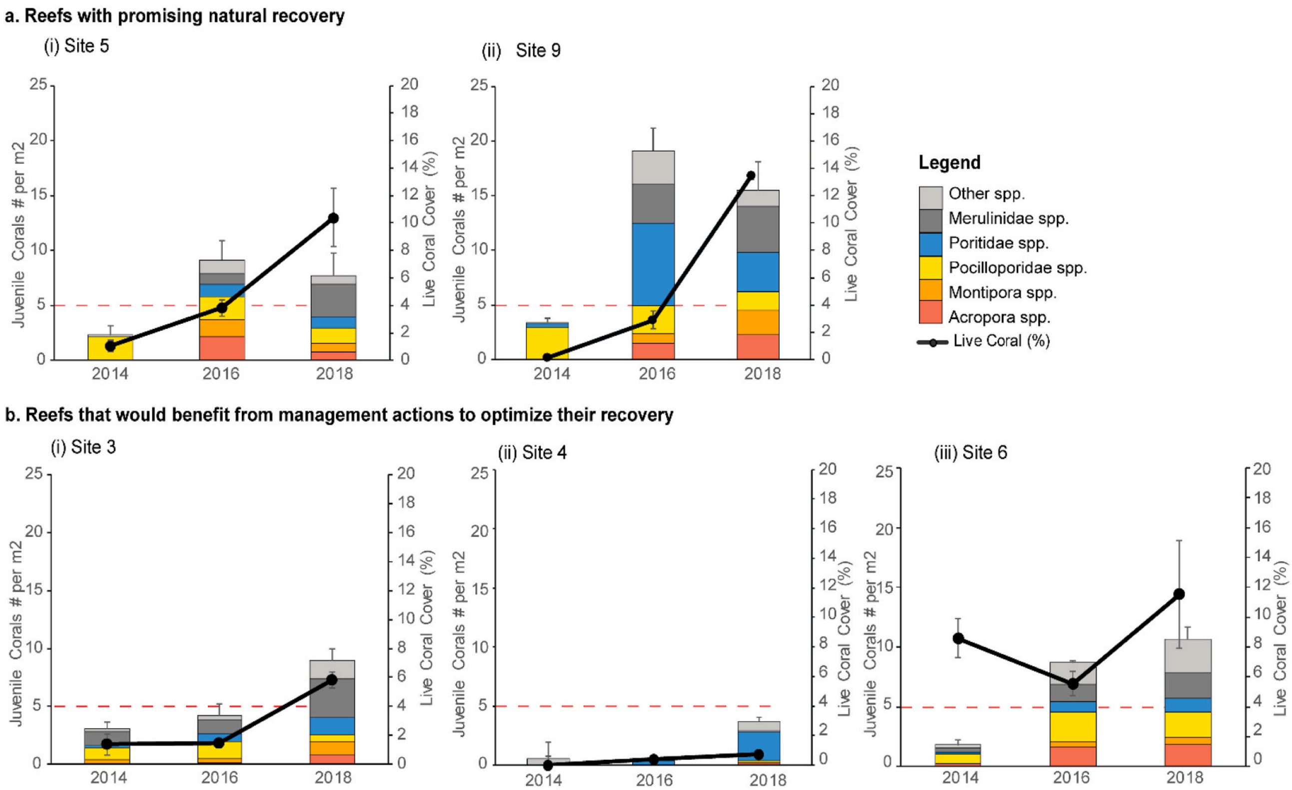

Fig. 5. Plots showing the temporal trends of juvenile coral density per m^2 (left y-axis) and overall live coral cover (right y-axis) at five highly valued reefs. Dotted line represents a likely threshold of juvenile corals needed to increase coral coverage but this would need to be verified with a larger reef sample size.

structural complexity, often associated with rubble fields. Therefore, conservation actions should primarily focus on assisting the stabilization process of rubble fields following appropriate practices (reviewed in Ceccarelli et al., 2020), while also focusing on increasing reef structural complexity at Sites 4 and 7. At the other sites, while there was a good coverage of suitable substrata for recruitment, the rugosity was low at Site 3 and could be improved. Lastly, herbivory was generally low throughout the eastern outer reefs, but macroalgal cover remained low, implying that herbivory is sufficient to limit macroalgal cover. Because the standing stock of herbivorous fish biomass is relatively low compared to the rest of Micronesia (Harborne et al., 2018), the causes of this are investigated (Supplementary Information) and adapted management recommendations are described below.

Overall, the standing stocks of targeted herbivorous fish are low (<5 g m^{-2}) on the eastern reefs (Table 4) compared to the broader Micronesian region, where medium to high stocks of the same fish species are reported to be between 8.5 and 80.5 g m^{-2} (Harborne et al., 2018). Yet, macroalgae did not dominate the eastern reefs. It is possible that the abundance of small fish and invertebrate grazers and scrapers that are not heavily targeted by the fisheries, together with good water quality, are helping to maintain low algal coverage. Following the typhoons, the structural complexity of reefs significantly declined as well as the biomass of bioeroding, commercially targeted herbivore, omnivore and piscivore fish (Supplementary Information). Overall, protection from fishing had a minor effect on fish biomass, with the only detected significant effect from protection on parrotfish size, found to be bigger in MPAs (n = 3) than at reefs open to fishing (n = 8). If fishing regulations were to be implemented across the eastern outer reefs, they should be stratified according to structural complexity (Mumby, 2016). Reefs with low complexity should be restored first (e.g. Sites 4, 6, and 7), while reefs with medium to high complexity could benefit from the implementation of local fisheries regulations to increase fish biomass to (1) improve grazing effect on algal turf and (2) limit the risk of a system phase-shift to macroalgal dominance. Such regulations would preferably include temporary fishing closures for key herbivorous fish since these fish populations can recover rapidly following closures (Mumby, 2006). However, considering the reliance by local communities on herbivore fishing in Palau (Bejarano et al., 2013), the implementation of subregion size or catch limits for key herbivores might be more appropriate (Prince et al., 2015).

At reef sites with suitable substrata for larval recruitment (Sites 3, 5 and 9, Table 4), further actions could help speed up coral recovery, and the quantification of larval supply and juvenile coral densities are useful. At sites where larval supply is normal and/or juvenile coral densities are above the threshold, conservation actions should focus on maintaining meta-population connectivity by ensuring that the key larval source reefs remain in good condition. Here, the strongest connectivity nodes were selected (Fig. 4) (Gouezo, 2019). Some strong larval sinks were initially defined on the eastern reefs for both *Acropora* and *Porites* corals as those that had average to above-average larval supply (Gouezo et al., 2021). Strong nodes were then identified as larval sources that had a probability of potential connectivity >0.8 to identified sinks. For the larval sources that had a probability of potential connectivity <0.8 but >0.1, reefs with the greatest number of connections (nodes-out degree) to key sinks were prioritized. The location of these key sources is displayed in Fig. 4.

Regulations at potential larval source locations could include limitations of reef trampling and boat anchoring enforced through regular patrolling of these reefs and the installation of mooring buoys for fishers, as well as reducing coral predation through the regular monitoring and control of *Acanthaster* spp. outbreaks. Only three larval sources were identified around Palau's main island (Babeldaob) and all of these are likely impacted by poor water quality (Golbuu et al., 2011). Local conservation efforts on land and around watersheds should be strengthened to minimize land erosion and runoff (Bartley et al., 2014), contributing to protecting these key larval sources.

At the five long-term monitoring study sites of the Palau International Coral Reef Center, no conservation actions have been undertaken

Table 5
Ecological indicators in monitoring programs, their pitfalls and suggested improvement to better inform management decisions during reef recovery.

Common ecological indicator	Indicator of	Pitfalls	Suggested improvement	References
Larval settlement on artificial substrata	Coral larval supply and settlement	Field and laboratory labour-intensive	Biophysical model in combination with the development of novel *in situ* larval assessment methods (e.g. *in situ* high-resolution macro-photogrammetry) following major spawning events	(Gouezo et al., 2021, this study)
Rugosity, structural complexity	Habitat space for corals and fish	Needs to be quantified at meso- and micro-scales	Visual or quantitative assessment for meso-scale and small-link chain method for micro-scale, or underwater structure-from-motion (SfM) photogrammetry methods, or hyperspectral imaging	(Ferrari et al., 2018; Harborne et al., 2012; Storlazzi et al., 2016; Wilson et al., 2007)
Percentage cover of benthic organisms (%) in quadrats or along transects	Benthic community status and trends	Limited reef area ≤50 m of benthos at a given depth (i.e. transect), haphazard sampling, time-consuming image/video analysis	Underwater SfM photogrammetry and hyperspectral imaging at georeferenced locations. Use of automated underwater vehicles to survey large reef area as well as deep reef slopes. Automated images annotation through artificial intelligence	(Armstrong et al., 2019; Beijbom et al., 2015; Gonzalez-Rivero et al., 2020; González-Rivero et al., 2016)
	Interactions with coral recruitment	Low levels of resolution on benthic images to detect cryptic interactive organisms	Need to be quantified at micro-scales (i.e. in 100–600 cm^2 quadrats) to define epilithic algal matrix characteristics (i.e. turf canopy cover and height, species assemblages, sediments trapping) and CCA cover	(Arnold et al., 2010; Birrell et al, 2005, 2008, 2005; Connell et al., 2014; Flower et al., 2017; Goatley et al., 2016)
Juvenile coral density (≤5 cm) per m^2	Recruitment success (coral settlement and post-settlement)	Low taxonomic resolution, no demography information	Tagging individual colonies and measuring size through time, or underwater SfM photogrammetry of tagged colonies or marked small permanent plots	(dela Cruz and Harrison, 2020; 2017; Doropoulos et al., 2015; Trapon et al., 2013)
Coral size structure and colony growth rate	Population size structure and growth	Not included in most monitoring programs: labour intensive, photogrammetry methods to quantify growth are new	Tagging individual colonies and measuring size through time, or underwater SfM photogrammetry of tagged colonies or marked large permanent plots	(Babcock, 1991; Edmunds and Riegl, 2020; Emslie et al., 2020; Figueira et al., 2015; Flower et al., 2017; Lirman et al., 2007; Storlazzi et al., 2016, (Lange and Perry, 2020))
Acanthaster spp. or *Drupella* spp. density per unit of area	Coral Predation	Threshold density per unit area for intervention	Define outbreak threshold for each system. (i.e. defined at 40 *Acanthaster* individuals per hectare on the Great Barrier Reef)	Moran and De'Ath (1992)
Fish species abundance and size estimate	Herbivory	Observer bias, not all herbivorous species are recorded	Use of stereo-video system to eliminate observer errors. Area-specific bite rates may be best to quantify grazing. Optional: Micro-invertebrates could also be recorded	(Goetze et al., 2019; Steneck et al., 2018)
Seawater properties Sedimentation Sea Surface Temperature Ocean acidification	Other stressors	Often not included but could influence recovery through chronic effects or episodic stress	Seawater sampling for particulate and dissolved nutrient and carbonate chemistry analyses, sediment traps (especially for reefs close to land runoff). *In situ* loggers for temperature	Fabricius (2005)
Coral diseases	Other stressors	Disease incidence often not quantified	In addition to disease prevalence, disease incidence could be quantified via monitoring diseased and healthy colonies through time	Flower et al. (2017)

since the typhoons' impacts in 2012–2013. This would represent a scenario where resources for managing recovery were unavailable. Only two reefs have displayed promising signs of early recovery: sites 5 and 9 (Fig. 5, a-i,ii) and both had juvenile coral densities >5 individuals m^{-2} and large coverage of suitable coral settlement substrata. The other three sites could benefit from management actions as described above to improve their recovery. For example, Site 6 (Fig. 5, b-iii) has had juvenile coral densities >5 individuals m^{-2} since 2016, but coral cover has varied between 8.5 and 11.5%. This site is a good larval sink (Fig. 4) but has a high cover of rubble (>70%) in between rocky boulders (Table 4). The mechanical instability of the rubble field that has not consolidated is likely causing elevated post-settlement mortality following coral settlement (Ceccarelli et al., 2020; Fox et al, 2003, 2019, 2003; Kenyon et al., 2020; Yadav et al., 2016).

5. Conclusions and further research

This discussion article provides a comprehensive overview on how the detection of key biophysical drivers can be incorporated into applied management actions that are contextualized to the ecological attributes of reefs with important social-ecological values. Long-term coral reef monitoring programs, both socioeconomic and ecological, provide valuable information to inform conservation management (e.g. Dacks et al., 2020; Houk et al., 2015). However, in the following final subsections and in agreement with previous studies (Flower et al., 2017; Lam et al., 2017), we highlight and discuss some limits in the quantification of key indicators, both social and ecological, that are needed to not compromise the proposed framework and improve the effectiveness of management actions during recovery.

5.1. Assigning socioeconomic values to reefs within a system

During the prioritization phase, the quantification of socioeconomic values of different reefs within a system was done using four main variables as proxies: access, fishing ground, cultural, and recreational. Alternatively, a more thorough valuation could be based on an ecosystem services valuation approach such as in Tamayo et al. (2018). However, it is likely that some essential market values such as for fisheries or tourism will not be available at the 'community' scale.

When socioeconomic values are not revealed by markets, reef valuation could be done through direct questionnaires (e.g. Laurans et al., 2013). Socioeconomic monitoring is often an integral component of coral reef monitoring programs in Pacific island nations (e.g., Micronesia Challenge; Nevitt and Wongbusarakum, 2013). These programs use indicators framed around fisheries, climate change and protective management to gauge the perceptions of conservation management by local communities. As reefs continue to degrade due to the increasing frequency of disturbances, the reefs that communities and stakeholders value the most need to be identified and monitored. For instance, it is quite common that the location of reef restoration activities is determined by one entity (e.g. a community group, a diving center) or in an arbitrary manner by the project leader(s), whereas it should be determined through a quantitative approach (Shaver et al., 2020). Hence, ecological questions on disturbance activities, reef degradation and reef recovery management (i.e., restoration activities) should be added to socioeconomic monitoring questionnaires, to help monitoring of the concept of 'shifting baselines' from a social perspective.

5.2. Improving coral reef ecological monitoring programs during recovery

Previous studies have highlighted the need to adapt coral reef monitoring programs that commonly describe ecosystem state and condition, to also include the quantification of key processes and drivers of change that are more useful for managing recovery. This is referred to as resilience-based monitoring (Flower et al., 2017; Lam et al., 2017). We have combined recommendations from the literature with this study into Table 5, defining the top ecological indicators needed to monitor coral reefs at present, as coral reefs are predicted to frequently be in early successional states after severe disturbances (Cheal et al., 2017; Hughes et al., 2018). We identify a major gap when monitoring coral reefs during recovery remains the quantification of larval supply in order to identify strong larval sinks. The identification of these zones can aid with the spatial prioritization and contextualization of management actions, and with our understanding of processes contributing to their resilience (Doropoulos and Babcock, 2018). Proxies of larval supply and settlement through space are quantified through larval assessments framed around the time of spawning events, but require long-term datasets with high spatial replication, that are both field and laboratory intensive and do not provide connectivity information. Therefore, larval supply assessments as well as data on juvenile densities, which integrate recruitment success across all stages and processes, should be combined with biophysical modelling when possible. While there is typically a high degree of heterogeneity in environmental conditions across coral spawning events leading to high inter-annual variability in larval supply, there is evidence that some reefs have consistently high and relatively even levels of larval supply through time (Gouezo et al., 2021). This is due to their location and hydrodynamic environment, leading to the concentration and retention of larval pools around them (Doropoulos and Babcock, 2018; Gouezo et al., 2021). The development of biophysical models can help to accurately define the location of these reefs, especially when predictions are validated by larval settlement datasets (Gouezo et al., 2021). Such development would help identify reefs that are supplied with high levels of larvae through time and their key sources that are needed for resilience-based management.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jenvman.2021.113209.

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