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RESEARCH ARTICLE

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Evaluating management strategies to optimise coral reef ecosystem services

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Abstract

1. Earlier declines in marine resources, combined with current fishing pressures and devastating coral mortality in 2015, have resulted in a degraded coral reef ecosystem state at Puakō in West Hawaiʻi. Changes to resource management are needed to facilitate recovery of ecosystem functions and services.
2. We developed a customised ecosystem model to evaluate the performance of alternative management scenarios at Puakō in the provisioning of ecosystem services to human users (marine tourists, recreational fishers) and enhancing the reef's ability to recover from pressures (resilience).
3. Outcomes of the continuation of current management plus five alternative management scenarios were compared under both high and low coral-bleaching related mortality over a 15-year time span.
4. Current management is not adequate to prevent further declines in marine resources. Fishing effort is already above the multispecies sustainable yield, and, at its current level, will likely lead to a shift to algal-dominated reefs and greater abundance of undesirable fish species. Scenarios banning all gears other than line fishing, or prohibiting take of herbivorous fishes, were most effective at enhancing reef structure and resilience, dive tourism, and the recreational fishery. Allowing only line fishing generated the most balanced trade-off between stakeholders, with positive gains in both ecosystem resilience and dive tourism, while only moderately decreasing fishery value within the area.
5. *Synthesis and applications*. Our customised ecosystem model projects the impacts of multiple, simultaneous pressures on a reef ecosystem. Trade-offs of alternative approaches identified by local managers were quantified based on indicators for different ecosystem services (e.g. ecosystem resilience, recreation, food). This approach informs managers of potential conflicts among stakeholders and provides guidance on approaches that better balance conservation objectives and stakeholders' interests. Our results indicate that a combination of reducing land-based pollution and allowing only line fishing generated the most balanced trade-off

between stakeholders and will enhance reef recovery from the detrimental effects of coral bleaching events that are expected over the next 15 years.

KEYWORDS
coral reef, decision-support tool, Ecopath with Ecosim, ecosystem services, ecosystem-based management, integrated ecosystem assessment, marine resources, socio-ecological trade-offs

1 | INTRODUCTION

Coastal systems are subject to multiple local pressures originating from land (e.g. sediment, pollutant and nutrient inputs) and sea (e.g. extractive activities, habitat destruction), and from global environmental change (ocean acidification, ocean warming, sea level rise; Mitchell, Jennerjahn, Vizzini, & Zhang, 2015). These pressures act simultaneously, degrading ecosystems and jeopardising the functions and services they provide (Brown, Saunders, Possingham, & Richardson, 2014; Burke, Reytar, Spalding, & Perry, 2011; Gilby et al., 2016). Effective strategies that maintain or improve the functioning and service provision of such systems are needed (Levin, Fogarty, Murawski, & Fluharty, 2009; McLeod, Lubchenco, Palumbi, & Rosenberg, 2005). Decision-support tools have been developed to address the often conflicting social, economic and ecological objectives across ocean users (Seppelt, Dormann, Eppink, Lautenbach, & Schmidt, 2011). The approach taken generally depends on the audience, area of interest, data availability, and the main objectives. For example, spatial analyses to prioritise areas where mitigation of land-based pressures would likely yield the best results led to the development of a global "hot spots" conservation map (Halpern et al., 2009). A more complex, local approach was taken by Gao and Hailu (2012), who used an integrated agent-based model with outcomes feeding into multi-criteria decision analyses to rank alternative management strategies based on ecological and human wellbeing. Another approach is to use Bayesian belief networks that incorporate stakeholder input to quantify risks associated with alternative management options (Ban, Graham, Connolly, & Biology, 2014; Gilby et al., 2016). Our approach utilised a trophodynamic ecosystem model to quantify the performance of alternative management actions based on indicators of three ecosystem services.

Coral reef ecosystems provide many ecosystem functions and services (e.g. habitats, buffers from waves, recreation) and are key components of coastal economies (Brander, Rehdanz, Tol, Van, & Van Beukering, 2012). Despite their importance, the condition of these resources has widely declined over the last few decades, especially close to population centres or where there are substantial land-based sources of pollution (De'ath, Fabricius, Sweatman, & Puotinen, 2012; Williams et al., 2015). A key focus of coral reef ecosystem management is to assess the ability of local management to both mitigate the cumulative impacts on reef ecosystem function and promote the sustainable provision of ecosystem services by improving reef resilience (Hoegh-Guldberg & Bruno, 2010). Resilience is the ability to absorb shocks, resist phase shifts, and regenerate after disturbances (Graham et al., 2006). Local pressures are exacerbated by global pressures (Burke et al., 2011; Hoegh-Guldberg, 1999), including three global "bleaching" events (i.e. the loss of corals' symbiotic zooxanthellae due to thermal stress), in 1998, 2010 and 2014–2016, during which many reefs have experienced high coral mortality (Wake, 2016). By mid-century, annual severe bleaching events are predicted to occur in about 70% of all reefs globally (Maynard et al., 2015), and by 2100, ocean warming is predicted to reduce coral habitat by 24%–50% (Cacciapaglia & van Woesik, 2015).

We applied a trophodynamic, coral reef ecosystem model that incorporates ecological complexity and the synergistic effects of multiple pressures and projected impacts of management changes to ecological and human wellbeing. We selected six management intervention strategies in collaboration with senior staff of the State of Hawaiʻi, Division of Aquatic Resources and evaluated their performance in relation to sustaining or improving three locally important ecosystem services: (1) ecosystem structure and resilience (system stability), (2) dive tourism (recreation) and (3) fisheries (recreation and food). Managers can use the results of this study to weigh trade-offs for different stakeholder groups and understand likely trends of their chosen scenario(s).

2 | MATERIALS AND METHODS

2.1 | Study site—Modelled area

Puakō, on the west coast of Hawaiʻi Island (Figure 1), has a large and well-developed fringing coral reef ecosystem (0–30 m) with historically high coral cover and fish biomass (Hayes et al., 1982) and has

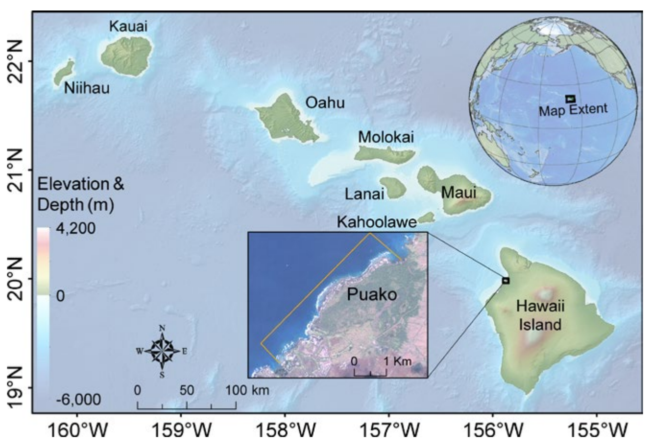


FIGURE 1 Location of Puakō on the west coast of Hawaiʻi Island. Orange rectangle (inset picture) identifies the geographic extent of the model domain

been widely used for a range of purposes. Fisheries regulations, established in 1985, prohibit the use of nets except throw nets and in the southern part of Puakō reef, the collection of aquarium species is also prohibited (Figure 1). Despite these regulations, between 1980 and 2007 coral cover and reef fish populations declined 35% and 50%, respectively (DAR, unpublished data 2007; Hayes et al., 1982) and then seemed to stabilise (The Nature Conservancy [TNC] unpublished data 2009, 2012, 2014). The fish community shifted with biomass decreasing for most harvested species. Concurrently, catch composition changed and reef fish landings decreased by about 20% between 1980 and 2007 despite a 3-fold increase in effort (Giddens, 2010; Hayes et al., 1982).

The human population of Puakō increased by 8% (from 397 to 429 people) between 1990 and 2000, then by another 80% (to 772 people) by 2010 (US Census Bureau). Throughout this period, most houses have had cesspools or septic tanks that contributed to elevated nutrients in nearshore waters (Couch et al., 2014). Overall, population growth and associated development, the increase of untreated wastewater, and more visitation due to improved accessibility have increased pressures on the coral reef ecosystems (Minton, Conklin, Weinant, & Wiggins, 2013). In addition, in 2015, prolonged elevated ocean temperature led to a severe regional bleaching event and *c*. 50% coral mortality around Hawai'i Island (Kramer, Cotton, Lamson, & Walsh, 2016).

Puakō has been exposed to pressures that many coral reef ecosystems face, including land-based sources of pollution, fishing and climate-induced coral mortality. Therefore, the modelling approach and conclusions drawn from this study are broadly applicable for coral reef research and local management.

2.2 | Ecosystem model components

We used the ecosystem model software Ecopath with Ecosim (EwE; version 6.4.4), which was created by Polovina (1984) and augmented by Christensen, Walters, Pauly, and Forrest (2008), and customised it to meet the needs of this study. The Ecopath component describes a system's steady state and structure based on a set of simultaneous linear equations describing the production and energy balance for each species group in the model (Christensen et al., 2008). Input values for these equations include the biomass, production to biomass ratio and consumption to biomass ratio for each group. If any one of these three values is not available, Ecopath can estimate it based on the other two and the "ecotrophic efficiency" value, which is the proportion of the production that is used within the system. Ecosim is the temporal component that estimates biomass flux between state variables as a function of time-varying biomass and harvest rates using coupled differential equations derived from the Ecopath equations (Christensen & Walters, 2004). Predator–prey interactions are moderated by vulnerability values that determine bottom-up (low vulnerabilities) or top-down (high vulnerabilities) control. Vulnerability values were obtained using Ecopath's "fit to series" option that uses a least-square fitting criterion for the residuals between predicted and observed time series. Input data for Ecosim included time series on fish biomass per functional group, fishery mortality, and effort per gear type. EwE is a mass-balanced model that treats the entire system as a single unit, and does not allow for variable distribution of model components (biological groups and stressors) in the modelled area.

The model start year was 1980, as this year has the first quantitative assessment of coral reef benthic and fish communities in Puakō (Hayes et al., 1982). Species were aggregated into 27 functional groups, 15 fish groups, 1 sea turtle group, 6 invertebrate groups, 4 primary producer groups, and 1 detritus group (Appendix S1). For fish functional groups, the vital rates (consumption to biomass and production to biomass ratios) and diet composition came from Fishbase, and Weijerman, Fulton, and Parrish (2013) and were calculated as a weighted mean based on the biomass of each species within that group (Appendix S2). Input values for invertebrates were recalculated based on Wabnitz et al. (2010), Weijerman et al. (2013) and references therein (Appendix S2). Sharks were not counted on survey transects, but were observed in the vicinity (Hayes et al., 1982). As sharks tend to be wary of divers around human population centres, they are likely underrepresented by visual surveys (Richards, Williams, Nadon, & Zgliczynski, 2011), and we included them as a low biomass group in the model.

We created linear time series of fishing effort per gear type based on creel surveys conducted in 1980 (Hayes et al., 1982) and in 2008 (Giddens, 2010) and extended this linear relationship to 2016. These surveys indicated that line fishing had increased by 2.3%, net fishing by 2.9%, and spearfishing (SCUBA and freediving) by 5.9%. For each species, we included a sale price and pooled these prices by functional group.

2.3 | Model customisation

Local pressures simulated in the model were fishing (net-, spear-, and line fishing) and land-based-sources of pollution (LBSP). We anticipate an annual increase in fishing effort of 1.2% in 2017–2032, based on projected population growth of 1.2% for Hawai'i County (DBEDT, 2006). Additionally, fishing effort in forecast model simulations varied based on the management scenario (Table 1). LBSP were assumed to be nutrients and bacteria from cesspools and septic tanks based on the human population increase and the continuing use of these on-site disposal systems, and the absence of overland rivers or streams as a clear point source for sediments and other pollutants (Minton et al., 2013). Survey data (Hayes et al., 1982, DAR unpublished data 2007) showed a clear decrease in coral cover between 1980 and 2007, but no clear trends in cover of different algal groups. We therefore restricted LBSP effects to only corals. Since Hawai'i Island had not been subjected to significant coral bleaching events before 2015 or other causes of large-scale coral mortality, we also assumed that observed earlier coral decline was caused by LBSP and simulated the decline of 35% of coral cover between 1980 and 2015 by forcing the model with a coral mortality. Ecopath simulates changes in biomass, and as we are interested in relative changes, for simplicity, we assumed that a 35% decline in biomass corresponded to a 35% decline in cover. We assumed an additional 10% coral biomass decline from LBSP in forecast scenarios based on a reduced rate of projected human population growth.

TABLE 1 Modelled management scenarios

Management scenario	Fishing effort	LBSP-related coral mortality
Current management	1.2% increase for line, net, and, spear fishing	10% decline in coral cover between 2017 and 2032
Only line fishing	1.2% increase in line fishing—no spear or net fishing	Same as above
No herbivore fishing	1.2% increase for all three gear types but no take of herbivorous fishes	Same as above
No take MPA	Entire Puakō area is a no-take MPA with zero fishing effort	Same as above
90% MSY	Fishing effort set to the level that maximises yield according to a precautionary ecosystem approach (*c*. 90% of MSY, see text for details)	Same as above
50% LBSP	1.2% increase for all three gear types	5% decline in coral cover between 2017 and 2032

As a global pressure, we simulated the 2015 bleaching event which caused a loss of 50% of coral cover (Kramer et al., 2016) and incorporated likely future bleaching events in 2021 and 2026 (van Hooidonk et al., 2016). As there is uncertainty about the severity of future ocean warming (Maynard et al., 2016), we simulated "high" (50%) and "low" (10%; Jokiel & Coles, 1990) bleaching-mortality scenarios to evaluate model sensitivity. Corals' recovery rates allowed for a recovery to 80% of pre-mortality cover in 10 years (Kolinski, 2007).

Coral reefs create structural complexity that provides refuge for small fishes. When reef-building corals die, the consequent loss of structure reduces a reef's ability to sustain the abundant and productive marine life that supports fisheries and underpins resilience (Rogers, Blanchard, & Mumby, 2014). We used the Ecosim "mediation" function to simulate this relationship with a sigmoid shape implying that with an increase in coral cover, the accessibility of the prey group to its predator decreases toward zero (Appendix S3).

The model was validated by verifying that a 100-year run with no perturbations produced stable trajectories, and calibrated by fitting biomass, catches and vulnerability parameters to historical biological and fishery survey data from DAR (unpublished data 2007) and TNC (unpublished data 2009, 2012, 2014) using EwE's least-square fitting criterion (Appendix S4).

2.4 | Simulations

Apart from the current management scenario, we simulated five intervention techniques: four alternative fishery management scenarios, and one land-based management scenario (Table 1). For all six simulations, we also included bleaching–related coral mortality under "high" (50% coral mortality) and "low" (10% coral mortality) severity climate scenarios. We did not adjust for possible shifts in gear use or effort allocation or for coral adaptation to higher temperatures.

2.5 | Determination of fishing mortality for 90% MSY scenario

The maximum sustainable yield (MSY), a reference point used by fishery managers to set control rules, is generally set at 80%–90% of MSY for a multi-species fishery (Worm et al., 2009). This precautionary MSY accounts for ecosystem dynamics, such as multispecies interactions, maintenance of biodiversity and genetic diversity, and reduction of waste (e.g. return of small individuals; Mace, 2001). To assess MSY for the multigear, multispecies fishery in Puakō, we incrementally adjusted effort of the three gear types simultaneously by the same amount relative to the 1980–2016 effort levels, and ran 30-year simulations. The relationship between effort and the corresponding sum of catches generated a multispecies surplus production curve with maximum catch being the MSY. Targeted groups in the fishery were targeted piscivores, invertivores, planktivores, browsers, grazers and parrotfishes (Appendix S1). From the surplus production curve, we selected a fishing effort that yielded *c*. 90% of MSY as the alternative management strategy "90% MSY" (Table 1).

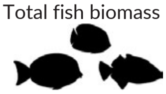
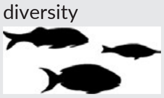
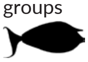
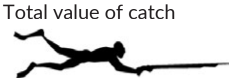
2.6 | Quantitative scenario comparison

Performance of the management strategies was based on variables indicative of ecosystem functions and services important to system stability and human well-being, namely (1) ecosystem structure and resilience (system stability), (2) dive tourism (recreation) and (3) fisheries (recreation and food; Table 2). We assessed the "best" performing strategy after 15 years based on the absolute change of each indicator between 2017 and 2032. Indicator values per ecosystem service were equally weighted to obtain an overall score. We also assessed how much better or worse the 3 ecosystem services would be in 15 years if an alternative scenario had been implemented now compared to the "Current Management" scenario.

3 | RESULTS

Relative comparisons across the management options were consistent under the two climate scenarios, indicating robust model behaviour. Quantitatively, indicators showed more pronounced trends (high or lower) under the higher severity climate change (Appendix S5). We will mainly focus on the high climate change severity scenario in the remainder of this section.

TABLE 2 Indicators reflecting ecosystem function and services used for performance evaluation of alternative management scenarios

Indicator	Rationale
(a) Ecosystem structure and resilience	
Coral cover 	A system that is dominated by corals offers more structure and will harbour more species diversity and higher species abundance (McClanahan et al., 2012)
Fleshy algal cover 	Fleshy macro- and turf algae compete with corals for space, inhibit coral recruitment and growth, and reduce coral survival (Hughes et al., 2007). Hence, a decline in fleshy cover is positive and an increase negative; therefore we report this indicator as the inverse of the value
Trophic level (TL) of fish community 	A high TL implies a lightly fished reef that is comprised of all trophic levels and hence all ecological functional roles that fish perform (Pauly, Christensen, Dalsgaard, Froese, & Torres, 1998)
Herbivore fish biomass 	Herbivorous fishes maintain algal assemblages in cropped states, which facilitates coral settlement and survivorship of coral recruits (Green, Bellwood, & Choat, 2009)
(b) Dive tourism	
Total fish biomass 	High abundance of fishes is highly rated by dive tourists (Grafeld et al., 2016). As a proxy for abundance, we used biomass
Fish functional group diversity 	Diversity is also highly rated by dive tourists. We used Ainsworth and Pitcher's (2006) method to calculate functional group diversity
Sea turtle and shark biomass 	Divers highly rate sightings of rare and charismatic species, such as sea turtles (unexperienced divers) and sharks (experienced divers) (Grafeld et al., 2016)
(c) Fisheries	
Sustainably harvested fish groups 	In stock assessments, a spawning potential ratio of >30% of the "pristine" (unfished) biomass is considered sustainable (Worm et al., 2009). We used the same concept but took a more precautionary approach and compared the number of functional groups with projected end (2032) biomass >40% of 1980 biomass
Marine trophic index (MTI) 	A decreasing mean trophic level of fisheries catch indicates a decline in abundance and diversity of higher trophic levels and highlights overexploitation (Pauly & Watson, 2005)
Total value of catch 	Even though most fishers do not sell their catches, we used this metric to quantify the obtained catches (opportunity benefit)

3.1 | Current management

Current fishery levels appear unsustainable, as most functional groups targeted by fisherman were projected to decline to very low levels. Ecosystem effects included a shift in the fish community towards undesirable species of piscivores (e.g. moray eels, hawkfishes), grazers (e.g. filefishes, tobies, Black Durgon), invertivores (e.g. porcupine fishes), planktivores (*Chromis* species) and small-bodied parrotfishes. Additionally, reef benthos was predicted to become dominated by algae and non-coral invertebrates. The surplus production curve shows that the current level of exploitation is higher than the effort level that would maximise sustainable yield (Figure 2). Reducing the fishing effort to 60% of the historic exploitation level would yield *c*. 90% of MSY, the target value for a precautionary ecosystem fishery. Ecosystem consequences of this reduced fishing effort included a 35% increase in target fish biomass and less or non-exploited groups decreasing by less than 4% (Figure 2).

3.2 | Evaluation of alternative management scenarios

Ecosystem effects of the management scenarios revealed that, generally, non-coral invertebrates, sea turtles and algal groups decreased in biomass under all management scenarios, other than "Current Management," but the opposite was true for most fish functional groups (Figure 3). Macro- and turf algal biomass declined

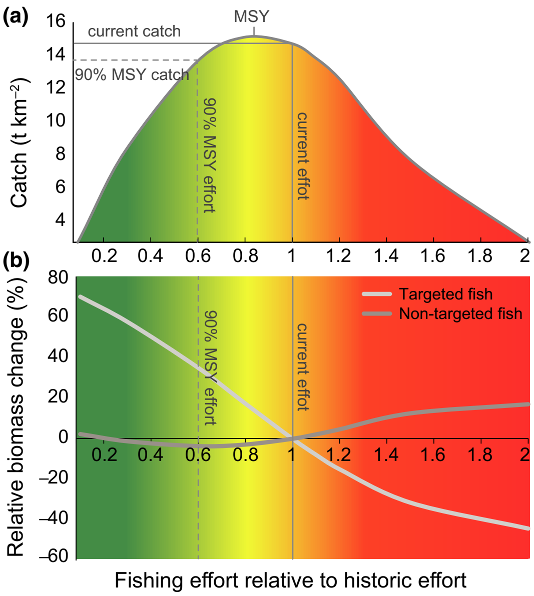


FIGURE 2 (a) Multispecies multigear catch equilibrium curve showing the relationship between the catches of species groups targeted by recreational fishers and incremental changes in fishing effort levels relative to historic effort. (b) Relative change in biomass of fish groups targeted and not targeted in recreational fisheries at different levels of fishing effort. MSY is maximum sustainable yield

most under the "No Herbivore Fishing" scenario (Figure 3) and, likely because fishing pressure was switched from targeted herbivores to other groups, target invertivores and target planktivores declined. Corals, corallivorous fishes and parrotfishes fared best under "50% LBSP," with a 30% increase in parrotfish biomass compared to 2017 (Figure 3).

Evaluating the ecosystem services by equally weighting their performance indicators under future high and low severity climate change simulations, showed that no single management scenario clearly outperformed all others in the 15-year timespan of this study (Figure 4, Table 3, Appendix S5). However, "Current Management" underperformed compared to all other scenarios. Ecosystem structure and resilience was most impacted by climate change due to the detrimental effects on coral cover (Table 3, Appendix S4). The fisheries ecosystem service had a similar response under the two severities while dive tourism actually benefitted from severe climate change especially under "Only Line Fishing" and "No Take MPA" (Table 3) due to the increase in sea turtles (Appendix S5). The "90% MSY" scenario resulted in the highest score for the fisheries ecosystem service while the "50% LBSP" scenario was the only one in which the total value of the catch did not decrease. The "No Take MPA" scenario, closely followed by the "No Herbivore Fishing" and "Only Line Fishing" scenarios, led to the greatest benefit for ecosystem structure and resilience (Table 3). Note though, that reducing LBSP ("50% LBSP" scenario) was the only scenario that led to an increase (19%) in coral cover in 2032 compared to 2017 but showed less than 7% change from 2017 for all other indicators (Figure 4). The "No Take MPA" scenario was most beneficial to dive tourism (Table 3). Overall, three fishery management scenarios ("No Herbivore Fishing," "Only Line Fishing," and "No Take MPA") improved most indicators at the cost of reduced total catch value (Figure 4).

The scenario with the highest positive results and low or no negative consequences was "Only Line Fishing." However, the value of catch decreased by 72% compared to "Current Management," which led to a negative value (−13.6%) for the fisheries ecosystem service (Table 3). The only management approach with no negative values for any of the ecosystem services was "90% MSY," but improvement of ecosystem structure and dive tourism was lower compared to "Only Line Fishing."

Evaluating the potential improvement in ecosystem functions and services in 2032 of local management compared to no additional management (i.e. "Current Management") under severe climate change, the ecosystem structure and resilience clearly benefitted the most of the three ecosystem services included (Figure 5). All five alternative management scenarios showed a 20%–50% improvement with "No Herbivore Fishing," closely followed by "No Take MPA" being the most effective. Effects on dive tourism ranged from −4% to 24%, with regulations that restricted fishing altogether or permitted only line fishing being the most beneficial while recreational fishers benefitted the most from reduced fishing effort (11% increase) or reduced LBSP (7% increase).

4 | DISCUSSION

4.1 | Ecosystem-based management

Recent studies have shown that local management can mitigate the negative effect of climate change on coral reefs (Selig, Casey, & Bruno, 2012; Thompson & Dolman, 2010) but it is less clear how to select effective management regulations and minimise conflicts among sectors. By incorporating the main pressures to coral reefs in an ecosystem model, we were able to assess the efficacy of alternative management strategies in improving ecosystem functions and services. Even under high severity climate change, local management could improve the ecosystem services evaluated. Permitting only line fishing showed the most improvement in the three ecosystem services overall under low and high severity climate change compared to "Current Management" with the ecosystem structure and resilience being the clear "winner" (33%–38% increase) at the cost of the fishery ecosystem service which declined by 14%.

Total catch is presently above the estimated MSY for Puakō's coral reef ecosystem, indicating that existing management regulations (i.e. "Current Management") have likely not effectively mitigated overfishing in the region. In addition, we found that "Current Management" underperformed compared to all alternative scenarios, providing further evidence that additional management is warranted to sustainably deliver ecosystem services in the future (Table 3, Figure 5).

The "No Herbivore Fishing," "Only Line Fishing," and "No Take MPA" management scenarios resulted in positive changes in key indicators of ecosystem structure and resilience. For example, herbivore biomass increased and fleshy algal decreased under all three scenarios, while the mean trophic level of the fish community—an indicator

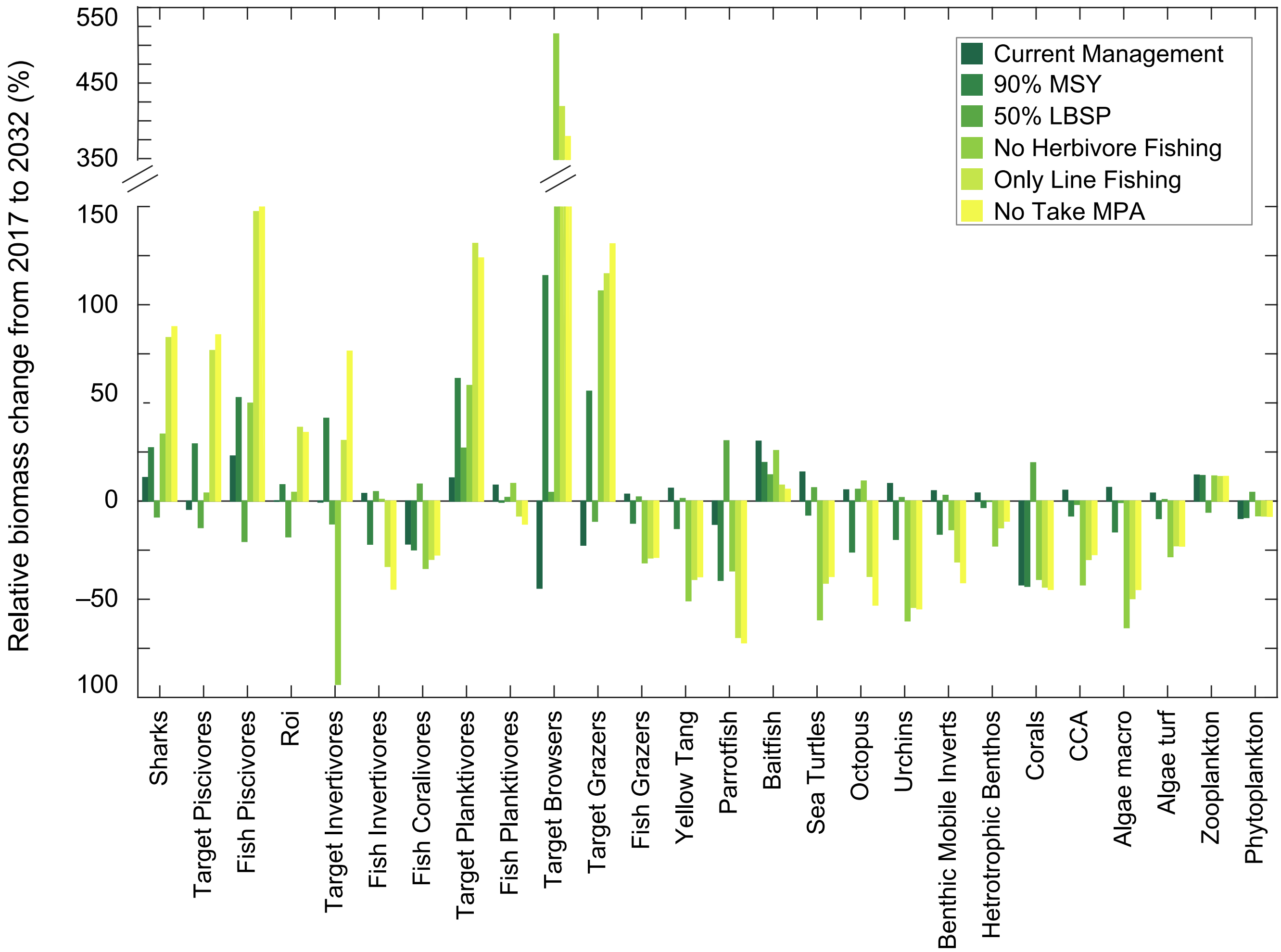


FIGURE 3 Biomass change of each functional group at the end of a 15-year forecast simulation relative to 2017 under high (50%) bleaching-related coral mortality

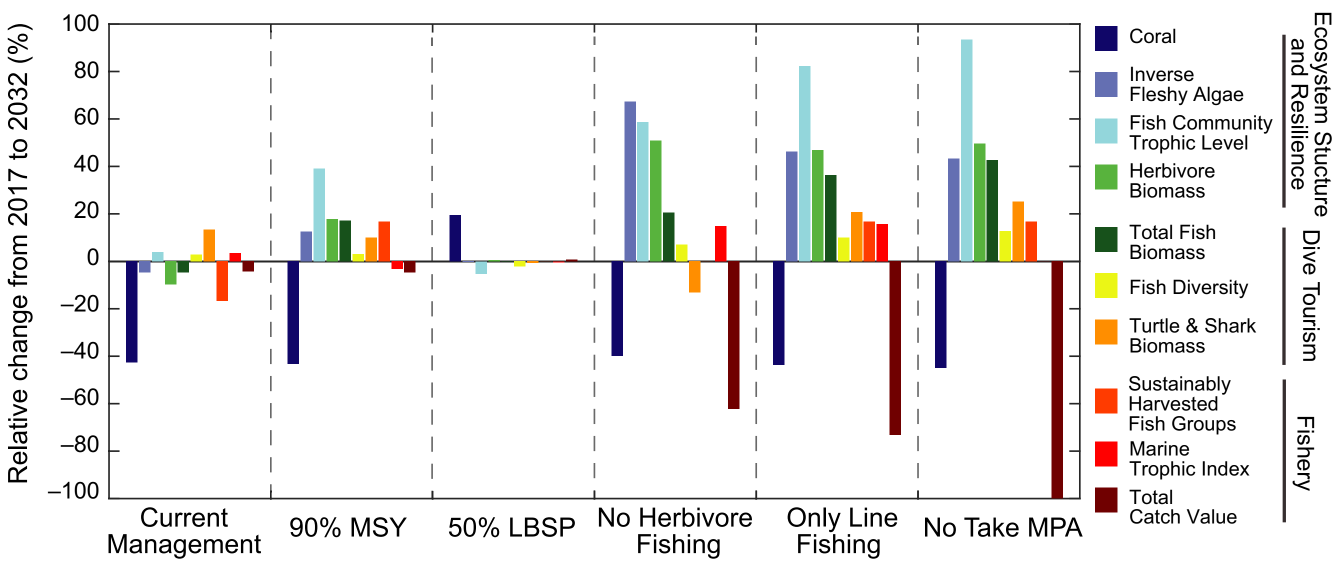


FIGURE 4 Relative change in absolute values between 2017 and 2032 for each of the indicators under different management simulations and a high (50%) bleaching-related coral mortality

TABLE 3 Decision support matrix for evaluating the effectiveness of alternative management scenarios in improving the current status of ecosystem functions and services in 15 years. All values are relative change at the end of the simulation period (15 years) compared to 2017 under (top value) a high (50%) bleaching-related coral mortality and (bottom value) a low (10%) bleaching-related coral mortality. Dark green indicates >15.1% improvement; light green 5.1%–15% improvement; yellow ±5% change; orange 5.1%–15% decline; and, red >15.1% decline

	Current management	90% MSY	50% LBSP	No herbivore fishing	Only line fishing	No take MPA
Ecosystem structure and resilience	−13.3%/−5.2%	6.5%/13.9%	3.6%/3.1%	34.2%/37.1%	32.9%/37.9%	35.4%/40.2%
Dive tourism	3.8%/2.2%	10.1%/7.4%	−0.9%/−1.4%	4.8%/3.8%	22.4%/18.4%	26.8%/22.2%
Fisheries	−5.8%/−6.1%	2.9%/2.4%	0.1%/0.0%	−15.8%/−16.7%	−13.6%/−14.2%	−27.8%/−27.8%

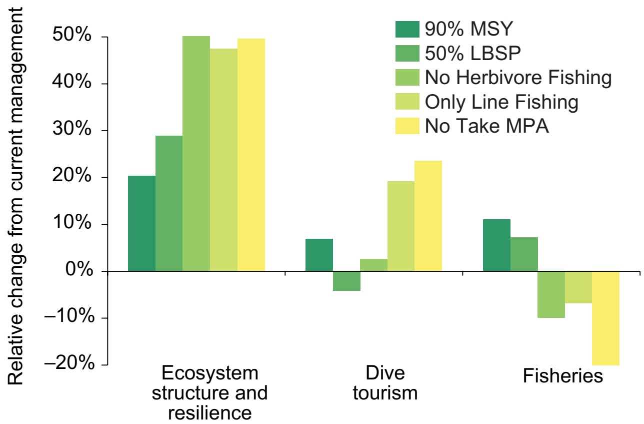


FIGURE 5 Relative difference between five alternative management scenarios and "Current Management" in their efficacy in improving ecosystem functions and services under high (50%) bleaching-related coral mortality in 2032

of reef fish functional diversity and redundancy—had the greatest increase under the "No Take MPA." The tradeoff of these approaches is reduced total catch value, which may result in conflicts with fishers. However, spill-over effects (Garry, Angel, & Aileen, 2003; Goñi et al., 2008) or enhanced reproductive output from larger individual fishes (Birkeland & Dayton, 2005) could provide increased fishing opportunities in connected areas and thereby reduce stakeholder conflicts.

Coral cover, an indicator for ecosystem structure and resilience, was found to decrease under most management scenarios as a result of coral bleaching-induced mortality. The "50% LBSP" scenario was the only management strategy in which coral cover increased, albeit modestly, facilitating greater coral recovery post-bleaching than other scenarios. It should be noted that indirect ecosystem effects of reef fishes on corals (e.g. increased biomass of large parrotfishes increases coral cover, increased biomass of grazers and browsers increases encrusting algae) although important for coral resilience and recovery (Heenan & Williams, 2013), were not accounted for in our model. We therefore likely underestimate the ecological benefits of increased reef fishes on the coral community, and potentially overestimate coral degradation, under all scenarios. Nevertheless, these findings highlight that a combination of fisheries regulations and reducing land-based pollution would improve coral reef ecosystem structure and resilience and thereby increase the potential to mitigate climate change impacts (Arias-Gonzalez et al., 2017; Weijerman, Fulton, & Brainard, 2016).

From a dive tourism perspective, coral reefs with high fish biomass and diversity and where charismatic species are present, are particularly attractive to divers (Grafeld et al., 2016). These indicators were highest for "Only Line Fishing" and "No Take MPA." However, a reef being very attractive to divers can also have negative consequences to the resident community, through overuse or overcrowding. On the other hand, dive tourism might help coastal communities adapt to fisheries limitations by providing opportunities from ocean-related activities, such as dive/snorkel businesses (Grafeld et al., 2016).

From a fishery sector perspective, "Current Management" would result in a decrease in key fishery indicators due to the projected increase in fishing pressure, driven by human population growth. Reducing the total fishery effort below the estimated MSY (i.e. "90% MSY") resulted in similar catch value as under "Current Management," but with increased fish biomass of functional groups targeted by fishers (Figure 2). Restricting fishing gears to "Only Line Fishing," while reducing total catch value, lead to the greatest gains in both the mean trophic level of catch and biomass of harvested fish groups. This management scenario also benefited key indicators related to Dive Tourism and Ecosystem Structure and Resilience, thereby representing the most balanced management approach of those we assessed.

4.2 | Assumptions and limitations

There are limitations in using models to inform policy (Plagányi & Butterworth, 2004). For example, only trophic effects can be simulated with an EwE model, and ecological benefits (e.g. spill-over effects, higher recruitment of older and larger fishes), indirect ecosystem effects, and benthic space competition are difficult or impossible to incorporate. Since this model application has no spatial component and was limited to <30-m waters, potential depth refuges from fishing, nutrients and ocean warming cannot be addressed. Similarly, it is impossible to incorporate spatial dynamics (e.g. migrations between different parts of the Bay). However, given the scale of Puakō Bay (*c.* 6 km shore line), our approach likely would not substantially affect model results. Additionally, climate projections indicate an increase in frequency of bleaching events over coming decades, leading to expected annual bleaching events by mid-century (van Hooidonk et al., 2016). Therefore, even with immediate implementation of "best" management strategies, corals may not be able to provide sufficient habitat for fishes to sustain high levels of fishery yield in the long term unless climate trends are ameliorated (Hughes et al., 2017) or if corals are able to adapt (Logan, Dunne, Eakin, & Donner, 2014; Rowan, 2004). Lastly, we were not able to account for differences in compliance and feasibility of enforcement for the various scenarios nor did we include changes in human behaviour (e.g. fishing effort) in response to ecosystem changes (e.g. Gao & Hailu, 2011).

Because of these limitations, model output data should be used for strategic management. By providing insights within a consistent setting, model outputs can be used to support decision-making, using explicit criteria among competing strategies (Dichmont et al., 2013; Metcalfe et al., 2015).

5 | CONCLUSIONS

No management solution simultaneously promotes recovery of ecosystem stability while also maximising the delivery of ecosystem services for Puakō, Hawai'i. Selecting the "best" management strategy for the region depends on the desired balance between enhancing ecological benefits (i.e. improved ecosystem structure and resilience) and improving socio-economic benefits to fishers and dive tourists. However, by elucidating tradeoffs, and by demonstrating the likelihood of improved outcomes from a range of potential management options, this study demonstrates that management strategy evaluation utilising ecosystem models is an important decision-support tool that can inform the natural resource management decision process.

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AUTHORS' CONTRIBUTIONS

M.W., J.M.G. and J.P.P. conceived the ideas and designed the methodology; W.J.W. and D.M. collected the data; M.W., J.M.G., J.P.P., I.D.W. analysed and interpreted the data; M.W. drafted the article and all authors contributed critical revisions to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

Model-specific input and output data are available from the Dryad Digital Repository https://doi.org/10.5061/dryad.4sh45 (Weijerman et al., 2018).

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