

RESEARCH ARTICLE

Climate change disturbances contextualize the outcomes of coral-reef fisheries management across Micronesia

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Abstract

Climate change is increasing disturbance events on coral reefs with poorly understood consequences for fish population dynamics and fisheries management. Given growing concerns over food security for the tropical Pacific, we assessed fisheries management policies across a suite of Micronesian islands since 2014 as climate disturbance events have intensified. Disturbances associated with the 2015–2017 ENSO led to significant mortality of corals and calcifying substrates and replacement with algae and detritus, followed by a doubling of biomass across all fish guilds that was proportional to their starting points for all islands. Increased fish biomass was equally attributed to growth of individuals evidenced by increased size structures, and recruitment/survival evidenced by larger population densities. However, the pulsed increase of fish biomass lasted 1–2 years for islands with limited and isolated MPA but remained high for islands with effective MPA networks for 4 years until the study ended. Meanwhile, policies to protect grouper spawning seasons resulted in increased occurrences that were magnified by disturbances and MPA. Grouper increases were largest where both spawning season bans and MPA networks existed, helping to tease apart the management-from-disturbance responses. Smaller rates of increases over longer time were observed for species with commercial fishing bans (bumphead parrotfish, Napoleon wrasse, and sharks). Yet, occurrences remain low in comparison to remote-island baselines, and MPA only provided benefits for juveniles in inner lagoons. Recent trends for these species were less influenced by climate disturbances compared to groupers. The results cautioned how short-term responses of fish assemblages following climate disturbances can provide false signs of success for some management policies without contextual reference baselines that may not exist. Positively, improvements were noted for both MPA and species policies in our region that are expected to benefit reef resilience.

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Introduction

Pacific island societies have coexisted with their marine resources for many generations using traditional forms of reef tenure that are diverse and often tailored to species, life stages and spawning events, taboo areas, and fishing methods [1–5]. Yet, human population growth, lack of employment options, technological advances, urbanization, and cash economies have placed a greater reliance on commercial fisheries with increasing top-down enforcement to try and control exploitation [6, 7]. Growing exploitation and reduced traditional knowledge can force management policies to become more streamlined to avoid confusion among stakeholders and address the logistical constraints of enforcement [8]. For instance, permanent no-take marine protected areas (MPA) have often replaced rotational/seasonal/ceremonial counterparts to cope with high fishing pressure and facilitate resilience [9], while harvesting bans for many large targeted species, such as bumphead parrotfish, may replace (temporary) customary harvesting policies [10]. Despite conservation gains in many localities, global studies continue to document declines in marine resources along human gradients that are now being influenced by climate change in poorly understood ways [11–13]. A deeper understanding of management efficacy and potential interactions with disturbance cycles is now critical as climate change intensifies.

Studies have predicted gradual declines in the physiological performance of fish as sea surface temperatures rise and ocean productivity decreases in the tropics across decades [14–16]. However, fewer studies have documented how climate disturbances have begun to reshape fisheries ecology within decades by altering the flux of energy through food webs following disturbances, leading to increased variability in fish abundances [17–19]. Small coral-associated fish decline in abundance and diversity following significant disturbances, but the pulsed algal/detrital influx following coral loss can benefit generalist herbivores and detritivores and lead to homogenization across habitats that lowers diversity [12, 20–25]. Yet, less consistent findings have been reported for larger fish that are targeted for food and essential for ecosystem resilience, such as parrotfishes, groupers, and snappers [16–18, 26, 27]. A meta-analysis that controlled for disturbance magnitude and time revealed: 1) temporary increases in herbivore biomass and density as corals died and algae and detritus increased, often perpetuating to higher level consumers and predators, 2) a shift from pelagic to benthic energy production within many primary consumers, and 3) potential long-term declines in fish biomass to levels below pre-disturbance periods that were associated with persistent changes in habitat structure [28]. Importantly, the positive response of target fish populations in the year(s) following coral mortality and algal/detrital accumulation has been described as a beneficial feedback loop between fish assemblages and reef substrates that supports ecosystem recovery [19]. However, it is unclear how fishing pressure and management policies may modulate this response [12, 26, 29]. More specifically, how do fisheries disturbance dynamics change when exposed to a growing portfolio of area-and-species based policies?

The present study examined temporal trends in fish assemblages across Micronesia, tropical North Pacific, during the past decade when MPA and species management policies evolved and climate change intensified. One significant driver of increased fisheries management has been the Micronesia Challenge (MC, 2006 to 2030) that represents a novel conservation movement defined by the leaders of five island nations across Micronesia to improve the ecosystem services offered to their societies [30]. Many islands established and improved MPA networks with dedicated enforcement. In addition, several species policies were developed to address declines in large targeted species. Many islands now have commercial sales ban for bumphead parrotfish, Napoleon wrasse, and sharks, as well as seasonal closures during spawning aggregations of large groupers [31–34]. We used 8 years of benthic and fish monitoring data to

evaluate the effectiveness of fisheries policies exposed to climate-induced disturbances associated with the 2015–2017 ENSO. Collectively, our study provided a contextual understanding of how fisheries management policies interacted with each other and interacted with climate disturbances that are becoming more common on coral reefs.

Methods

Micronesia is comprised of many tropical nations that together account for over 6,000 km² of coral reefs [35]. Past studies documented that unsustainable fishing and land-based pollution represented primary chronic stressors that have impacted Micronesia's marine resources in recent decades [19, 32–34, 36–38]. Houk et al. [37] further reported that fishing pressure had a disproportionate impact to both fishery resources and overall coral-reef ecosystem condition, while proxies to land-based pollution were noted as secondary drivers in lagoon environments adjacent to urbanized watersheds. Micronesia reefs are also facing increasing frequencies of acute disturbances tied to climate change [39]. Most recently, heat-stress disturbances during the 2015–2017 ENSO have reduced living coral cover by up to 90%, with similar magnitudes of degree heating weeks and impacts on Chuuk, Pohnpei, and Kosrae. Yap experienced unique low level heat stress in late 2014 that was not related to the 2015–2017 ENSO, and then experienced high densities of Crown-of-Thorn starfish in 2015 that coincided with the onset of ENSO (densities ranged between 0 to 6 individuals per 100 m² during the annual monitoring event, with a mean of 1±0.80 SD per site). The noted disturbance regimes caused similar 15 to 20% losses of corals and/or other calcifying substrates including crustose coralline algae and soft corals, with replacements of turf, macroalgae, and cyanobacteria (S1 Fig). Previous work also documented differential coral loss across Micronesia associated with the recent ENSO based upon taxonomy [39]. Here, we examined fish assemblage responses to ongoing fisheries management policies and the bottom-up pulses of algae and detritus provided to the coral-reef food webs following disturbances.

We first evaluated MPA efficacy and the status of several species-specific fisheries policies across the main islands of the Federated States of Micronesia (Yap, Chuuk, Pohnpei, and Kosrae) (Fig 1, S1 and S2 Tables). Marine protected area (MPA) networks were established and enhanced around Yap and Pohnpei during three distinct time frames: i) most were initiated between 2010 and 2013, Yap-3, Pohnpei-5, ii) one was initiated in 2015 in Pohnpei, and iii) two were established between 2018 and 2020, one each on Yap and Pohnpei (Fig 2 and S1 Table). Individual smaller MPA were also established in Chuuk and Kosrae but given their isolation to inner reefs these were omitted from our island-scale MPA analyses within. Second, several local and regional fisheries policies were investigated: 1) a ban on commercial harvesting of *Bolbometopon muricatum* (established in 2008, 2010, 2012, 2015 for Kosrae, Chuuk, Pohnpei, and Yap, respectively) and *Cheilinus undulatus* (2010, 2015, and 2019 for Chuuk, Yap, and Pohnpei, respectively), 2) a ban on harvesting groupers during their spawning season in Pohnpei since 2012 and Chuuk since 2015, and 3) a regional ban on shark fishing for all study islands similarly since 2015. Collectively, these species are referred to as large targeted species with active management policies.

Data collection

Data were collected by all authors in a collaborative partnership with the Micronesia coral-reef and fisheries monitoring network (<https://micronesiareefmonitoring.com/>). Data were deposited into the Micronesia Reef Monitoring online database that hosts data, provides data access, and offers collaboration with interested individuals and organizations (<https://micronesiareefmonitoring.com/>). Data are also publicly available through the National

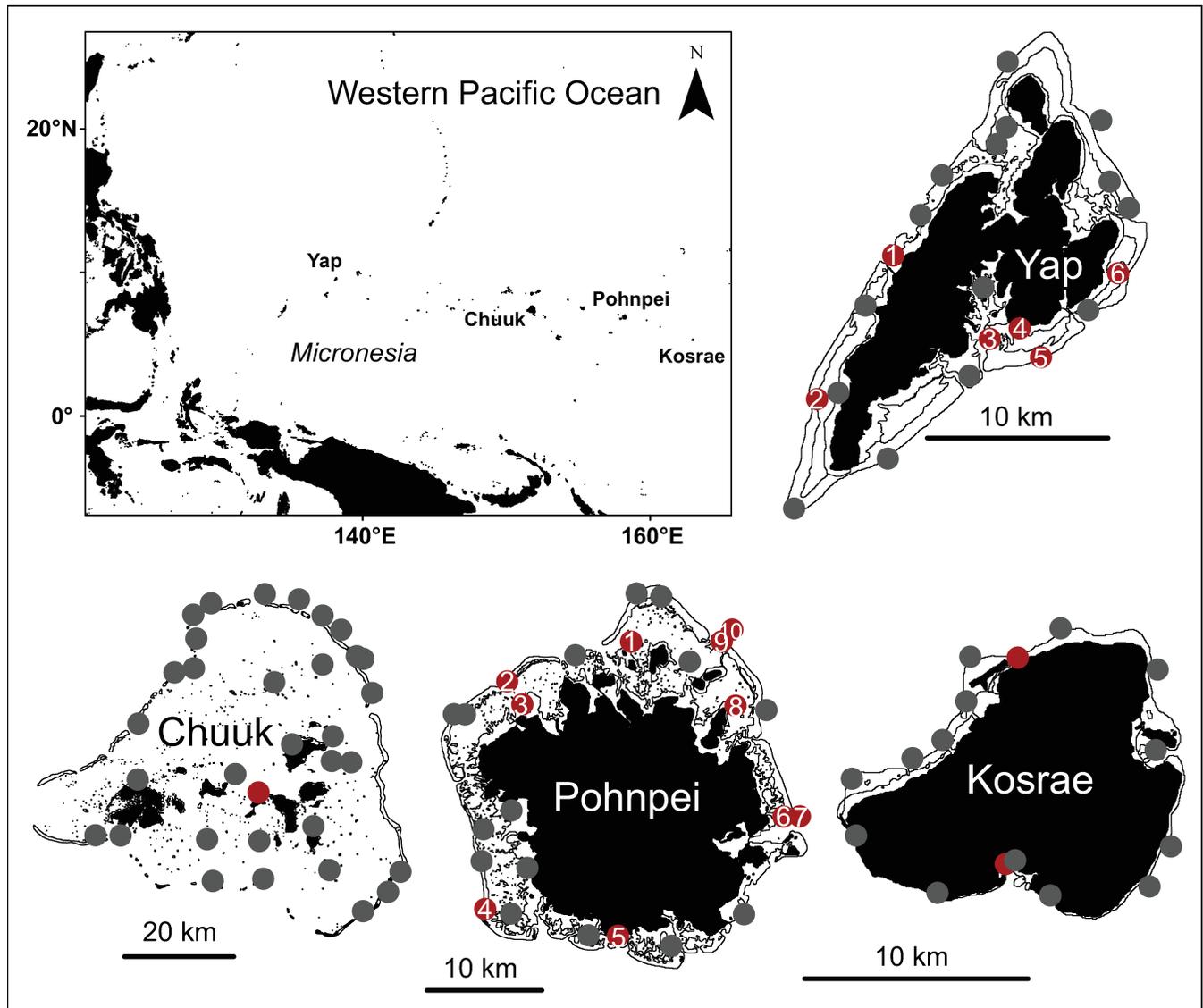


Fig 1. Map of Micronesia and the main populated islands of the Federated States of Micronesia: Yap, Chuuk, Pohnpei, and Kosrae. Red dots represent no-take marine protected areas (MPA) with numbers for Yap and Pohnpei corresponding to Fig 3, gray dots represent non-MPA. The coral reefs base layer is available through the Allen Coral Atlas project (<https://www.allencoralatlas.org/>, Allen Coral Atlas maps, bathymetry and map statistics are © 2018–2022 Allen Coral Atlas Partnership and Arizona State University and licensed CC BY 4.0 (<https://creativecommons.org/licenses/by/4.0/>)). The land base layer was made by the authors based upon the Allen Coral Atlas products.

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Oceanic and Atmospheric Administration National Center for Environmental Information website (<https://www.coris.noaa.gov/search/catalog/main/home.page>) under accession number 0162463. No permits were required because our work was non-invasive and did not require and collections of marine specimens. Long-term monitoring site selections were stratified across (i) management regimes, (ii) wave exposure, (iii) islands, and (iv) major reef habitats, to be representative of each island [37], with the total number of sites proportional to the area of reef habitat (Fig 1). Therefore, statistical analyses of temporal trends at the island and reef type scales were based upon the same suite of sites, which were indicative of the environments and management regimes of our study islands. This approach controlled for inherent

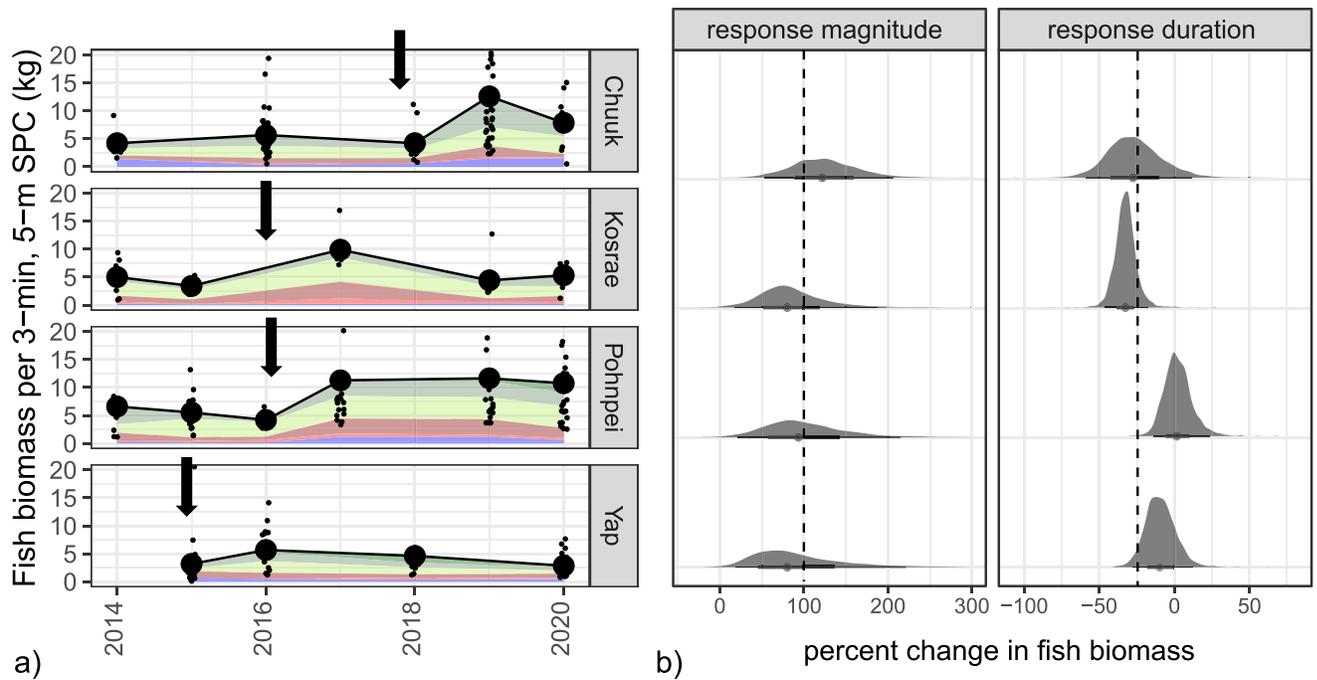


Fig 2. Trends in fish biomass from spatially-restricted fish surveys (a). Colors indicate fish guilds: darkest green—bumphead parrotfish, green—large herbivore and detritivores, light green—small herbivore and detritivores, dark red—large secondary consumers, light red—small secondary consumers, blue—tertiary consumers. See [methods](#) for fish guild details. Black arrows indicate the timing of disturbances. Small black dots represent individual reefs while large black dots indicate annual means. Posterior distributions from Bayesian modeling of the magnitude of the fish response, or the change in fish biomass 1-year after mass coral mortality compared to before, and the duration of fish response measured by the change in fish biomass 3-years following mass bleaching compared to before (b). For Chuuk, data were only available 2-years following the disturbance but statistical analyses for the response duration were all scaled to change in fish biomass per year.

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differences in site-based characteristics (i.e., rugosity) to the extent possible, allowing for an evaluation of island-scale policies. Cumulatively, the present study included fisheries data from 95 sites across Micronesia collected between 2014 and 2020.

The sizes and abundances of target food-fishes were collected using standard visual census techniques by experienced and calibrated observers. Food-fish were defined as acanthurids, scarids, serranids, carangids, labrids, lethrinids, lutjanids, balistids, kyphosids, mullids, holocentrids, and sharks. Fish surveys were conducted using 12 stationary-point counts (SPCs) separated by equal intervals along 5 x 50 m transect lines established at each site and used for benthic data collection noted below. During each SPC, the observer recorded the species and estimated the size of all fish within a 5 to 6 m circular radius for a period of 3-minutes. Fish sizes were binned into 5 cm categories and converted to biomass using coefficients from regional fishery-dependent data where available [19, 32, 36], or else from FishBase (www.fishbase.org). Total biomass and biomass across size-based trophic guilds were derived from these surveys, with guilds previously defined by trophic level and maximum body sizes [19]. The spatially-restricted data described above were available from 2014 to 2020.

Because large targeted fish often avoid observers and may not be well captured in the spatially-restrictive surveys, a second spatially-unrestricted method was adopted in 2020. The second observer maintained a distance of 5 m behind the primary observer and conducted 3-minute SPC fish counts of all fish larger than 40 cm with no spatial restrictions. The species examined by this study included: 1) *Bolbometopon muricatum* or bumphead parrotfish, 2)

Cheilinus undulatus or Napoleon wrasse, 3) large groupers consisting of *Plectropomus* spp. and *Epinephelus* spp. with asymptotic sizes greater than 40 cm, and 4) sharks (*Carcharhinus amblyrhynchos*, *Triaenodon obesus*, and *Carcharhinus melanopterus*—grey-reef, white-tip, and black-tip sharks). In addition, we transcribed data from rapid ecological assessments that were conducted in the mid-2000's for the islands of Yap and Pohnpei to gain a unique historical perspective for potential shifts in bumphead parrotfish and Napoleon wrasse that were observed [40, 41]. Historical species checklists represented presence/absence data for each site based upon similar dive profiles as our study. Thus, historical data were similar to spatially-unrestricted observations conducted in 2020 once aggregated to the site level and converted to presence/absence data.

Last, previously published benthic data were summarized to investigate the connection between the disturbance events, the subsequent increase in non-calcifying algal/detrital substrates that emerged as corals and other calcifying organisms died, and the increases in both fish density and biomass shortly after disturbances [39]. Benthic data were collected from standardized photographs taken at 1 m intervals on the transect lines, with benthic substrates recorded under 5 randomly placed dots from each photo (S1 Fig, see [42] for further details).

Data analyses

Data were analyzed to address three main questions. First, what were the responses of fish assemblages to major coral bleaching events for islands with and without MPA networks? Our hypothesis was that islands should have similar, pulsed increases in fish biomass following disturbance events that removed corals and other calcifying substrates that were replaced with algae and detritus [12, 17]. However, we hypothesized that effective MPA networks may lead to greater pulsed increases following coral bleaching or longer durations of elevated fish biomass due to increased recruitment and/or growth. Our data were multilevel as SPC replicates were nested into sites, and sites were nested into islands that were compared across three discrete disturbance periods (before, 1-year after coral bleaching, and 3-years after coral bleaching). We therefore used a Bayesian linear mixed-effects model to predict fish biomass differences between disturbance periods for each island. This statistical model is akin to an ANOVA comparing fish biomass across the disturbance periods, however, is more appropriate because it accounts for the potential influence of random site-level variation (i) and fixed variation from disturbance periods (j). Therefore, the model assumed log-normal data distributions and multilevel nesting of individual SPC's within their respective sites as random variation (i).

$$\text{fish biomass} \sim \text{LogNormal}(\mu_{ij}, \sigma_i) \quad (1)$$

$$\mu_{ij} = \alpha_{\mu} + \alpha_{\text{Site}_{[i]}} + \beta_{\text{DisturbancePeriod}_{[ij]}}$$

This model described fish biomass based upon a lognormal distribution with terms for the overall mean effect size (μ_{ij}) and associated standard deviation (σ_i). To fit our posterior distributions, we used mildly informative and conservative priors for the intercepts α_{μ} and standard deviations for all model parameters—Student-t(3, 0, 4.5). Numbers respectively indicate the degrees of freedom, location, and scale associated with the Student-t distribution used for priors. In sum, this process developed a posterior distribution describing potential change in fish biomass 1-year and 3-years post disturbance for each island that was evaluated against the null hypothesis that no changes occurred.

Our second question asked whether MPA networks established on two study islands, Yap and Pohnpei, have been successful in enhancing fish biomass through time? The efficacy of

MPA were examined visually by plotting temporal biomass trends and associated confidence intervals against a suite of reference sites in similar habitats where fishing occurs legally. This provided an indication of MPA status through time, with significance inferred by the degree of confidence interval overlap between reference sites and MPA across the study years. MPA effects were calculated as the percent change in biomass between the year established and 2020. Interestingly, no relationships existed between MPA size or longevity and the changes in fish biomass, and thus, MPA size and longevity were not part of our results, although were reported (S1 Table).

Our third question asked whether policies to protect several large targeted species have been successful through time, and if success depended on MPA status or disturbance period? The counts of large targeted species observed in spatially-restricted SPC data were examined using Bayesian mixed-effects models because they were multilevel and zero-inflated to varying degrees. Bayesian models for large-bodied groupers, which were more common compared to other large targeted species, were developed using the zero-inflated negative binomial distribution (ZNBI). Data were converted to presence/absence per SPC survey, and the dependent variable represented the number of SPC's where individuals were observed (i.e., site-based counts). The model structure used to estimate the occurrence of large groupers on SPC surveys between 2014 and 2020 included island as a fixed factor because policies for grouper management differed by island. The model also incorporated MPA status as a fixed factor and reef type as a random factor (i).

$$\text{SPC grouper counts} \sim \text{ZNBI}(z_{ij}, \lambda_{ij}) \quad (2)$$

$$\text{logit}(Z_{ij}) = \alpha_z + \alpha_{\text{reeftype}[j]} + \beta_{\text{year:island:mpa}[j]}$$

$$\text{LogNormal}(\lambda_{ij}) = \alpha_\lambda + \alpha_{\text{reeftype}[j]} + \beta_{\text{year:island:mpa}[j]}$$

This model described grouper counts using the ZNBI with effect sizes split across two terms: 1) the degree of zero-inflation (z_{ij}), or probability of encountering a grouper, based upon a logit distribution, and 2) the shape (λ_{ij}), describing the predicted grouper counts given a non-zero probability of encounter, based upon a lognormal distribution. We used mildly informative and conservative priors: $z_{ij} \sim \text{Beta}(1, 1)$; $\lambda_{ij} \sim \text{Gamma}(0.01, 0.01)$; $\alpha_{\lambda_{zi}} \sim \text{Student-t}(3, 0.7, 2.5)$, with all standard deviation estimates (σ) $\sim \text{Student-t}(3, 0, 2.5)$. In sum, this model combined the probability of encountering a large grouper with the estimate for their density to predict annual estimates for each island and reeftype that were examined through time, akin to an ordinary linear regression but while accounting for the nested data structure and the zero-inflated distributions.

Other large targeted species were less common compared to groupers. Bayesian models for other species were developed using the binomial distribution, which estimates a probability, between 0 and 1, that a large targeted species would be observed at any given site. Data were aggregated to the site level and our dependent variable was presence/absence per site instead of SPC replicate. The model structure was similar to above, however, our model comparison process described below revealed no dependence on MPA status for these species. Thus, MPA was removed from the below equations.

$$\text{site occurrence} \sim \text{Binomial}(1, p_{ij}) \quad (3)$$

$$\text{logit}(p_{ij}) = \alpha_p + \alpha_{\text{reeftype}[j]} + \beta_{\text{year:island}[j]}$$

This model described counts using the binomial distribution with a logit-link function to

estimate the parameter (p_{ij}). We used mildly informative and conservative priors: $\alpha_{pi} \sim \text{Student-t}(3, 0, 2.5)$, with all standard deviation estimates (σ) $\sim \text{Student-t}(3, 0, 2.5)$. In sum, this model predicted annual estimates describing the probability of observing an large targeted species for each island and reef type that were also examined through time, akin to a regression.

Finally, similar presence/absence comparisons for two large targeted species, bumphead parrotfish and Napoleon wrasse, were examined with respect to novel baselines from rapid ecological assessments conducted in the mid-2000's on Yap and Pohnpei [40, 41]. These past data represented site-based presence/absence in the form of species checklists that were comparable with spatially-unrestricted observations conducted in 2020 once aggregated to the site level. The probabilities of encountering these large targeted species were contrasted between 2020 and the mid-2000's using the same binomial modeling process described above.

All Bayesian models were created in Stan computational framework (<http://mc-stan.org/>) accessed with brms package [42]. Models were compared and inspected against null model counterparts that predicted no change to identify significant trends, and model structure was examined using the widely applicable information criterion and leave-one-out cross validation process as metrics of improving the model fit and stability [43]. Competing models were also examined for chain convergence using R-hat values.

Results

Thermal stress and high Crown-of-Thorn starfish densities between 2014 and 2017 removed corals, crustose coralline algae, and soft corals and led to a 15 to 20% increase in algae and detritus that was followed by a doubling of fish biomass around FSM study islands (Fig 2, S1 and S2 Figs, comparisons of fish biomass before disturbance versus 1-year after, termed the response magnitudes). Fish biomass increases were noted across all trophic guilds and were proportional to pre-disturbance starting points. Interestingly, biomass increases were attributed to a mean 20% increase in the assemblage size structure, that equated to ~75% increase in growth-biomass when averaged across guilds, and a mean 66% increase in density-biomass (S2 Fig). Supporting contrasts of Bayesian posterior distributions confirmed a ~100% increases in overall fish biomass for all islands in the year following disturbance, or a doubling, with overlapping 66% confidence intervals that suggested no significant differences existed in response magnitudes (Fig 2B, complete convergence of Bayesian models). However, the duration of increased fish biomass differed as islands with MPA networks appeared to have longer-lasting responses. In support, direct contrasts between MPA and non-MPA reefs suggested sustained increases in fish size for all major fish guilds and sustained increases in density for primary and secondary consumers on MPA reefs compared to non-MPA three years following disturbances (S2 Fig).

Yap had four MPA with fish biomass consistently above reference baselines in 2016 for most reef habitats (Fig 3A), but localized declines were evident in recent years. Meanwhile, Pohnpei had six MPA with biomass increasing over the study years relative to reference baselines, and now represents the most effective network (Fig 3B). Interestingly, MPA efficacy was not dependent upon size or when the MPA was established (S1 Table), but previously related to social structure and enforcement capacity (*discussion*). Pohnpei and Yap islands with MPA networks had greater response durations compared to other islands, measured by the change in fish biomass before compared to 3-years post disturbance (Fig 2A and 2B). In support of fisheries management influencing the response durations, the declines in fish biomass following the disturbances were mainly due to decreased densities of fish, especially in non-MPA reefs, but not decreased size structure (S2 Fig).

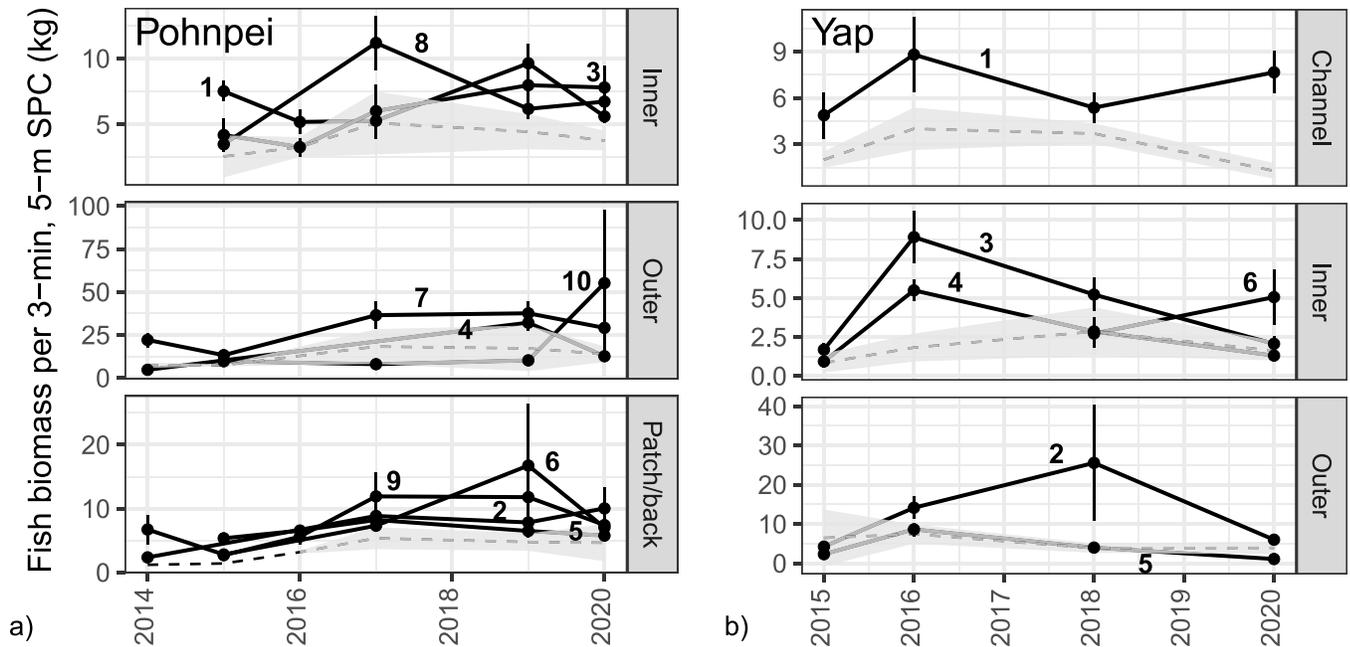


Fig 3. Trends in fish biomass for Pohnpei (a) and Yap (b) MPA networks. Numbers correspond with MPA trendlines identified in Fig 1, with standard error bars associated with each site-year. Mean biomass from all references sites in similar reef habitats are depicted by the faint dashed line with grey confidence intervals representing the standard deviation among sites. Black arrows indicate disturbances.

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Large targeted species trends

Groupers were the most abundant large species investigated with active protection of spawning aggregations in Pohnpei since 2012 and Chuuk since 2015. Occurrences of large groupers gradually increased between 2014 and 2020 based upon spatially-restricted data, however, trends were dependent upon island, MPA status, and reef type. The probability of observing a large grouper on a replicate SPC survey increased from 14 to 24% in Chuuk across the study years, with highest occurrences noted for outer reefs (Fig 4, posterior estimate of annual increase $9 \pm 3\%$ SD, complete convergence). Interestingly, significant increases were also observed in Pohnpei, but were strongly dependent on MPA status. The probability of observing a large grouper increased from 13 to 50% in Pohnpei MPA across the study years, with notable gains in all major reef types (Fig 4, posterior estimate of annual increase $20 \pm 3\%$ SD, complete convergence), especially for patch and inner fringing reefs. Non-MPA reefs in Pohnpei had notable gains for patch/back reefs, but diminished gains elsewhere that limited the overall increase to $4 \pm 3\%$ SD. Non-significant increases in groupers existed on remaining islands as confidence intervals associated with slope estimates crossed zero, suggesting high variation led to non-significant responses.

All other large species with commercial harvesting bans, but not subsistence fishing bans, were rarely encountered in spatially-restricted data. Binomial models predicting presence/absence at the site level revealed fewer significant trends. Models for shark occurrences revealed a 47% increase for all reef types in Pohnpei, and ~20% increase for Chuuk outer and channel reefs, with very limited observations for other islands and reef types (Table 1, Fig 5). Shark occurrences were not influenced by MPA status. Bumphead parrotfish increases were mainly driven by the rise in occurrences from 25 to 42% in Yap, and less substantial increases in Pohnpei, representing the two high islands with most extensive inner lagoon habitat favorable for this species (Table 1, Fig 5). Bumphead parrotfish occurrences in spatially-restricted

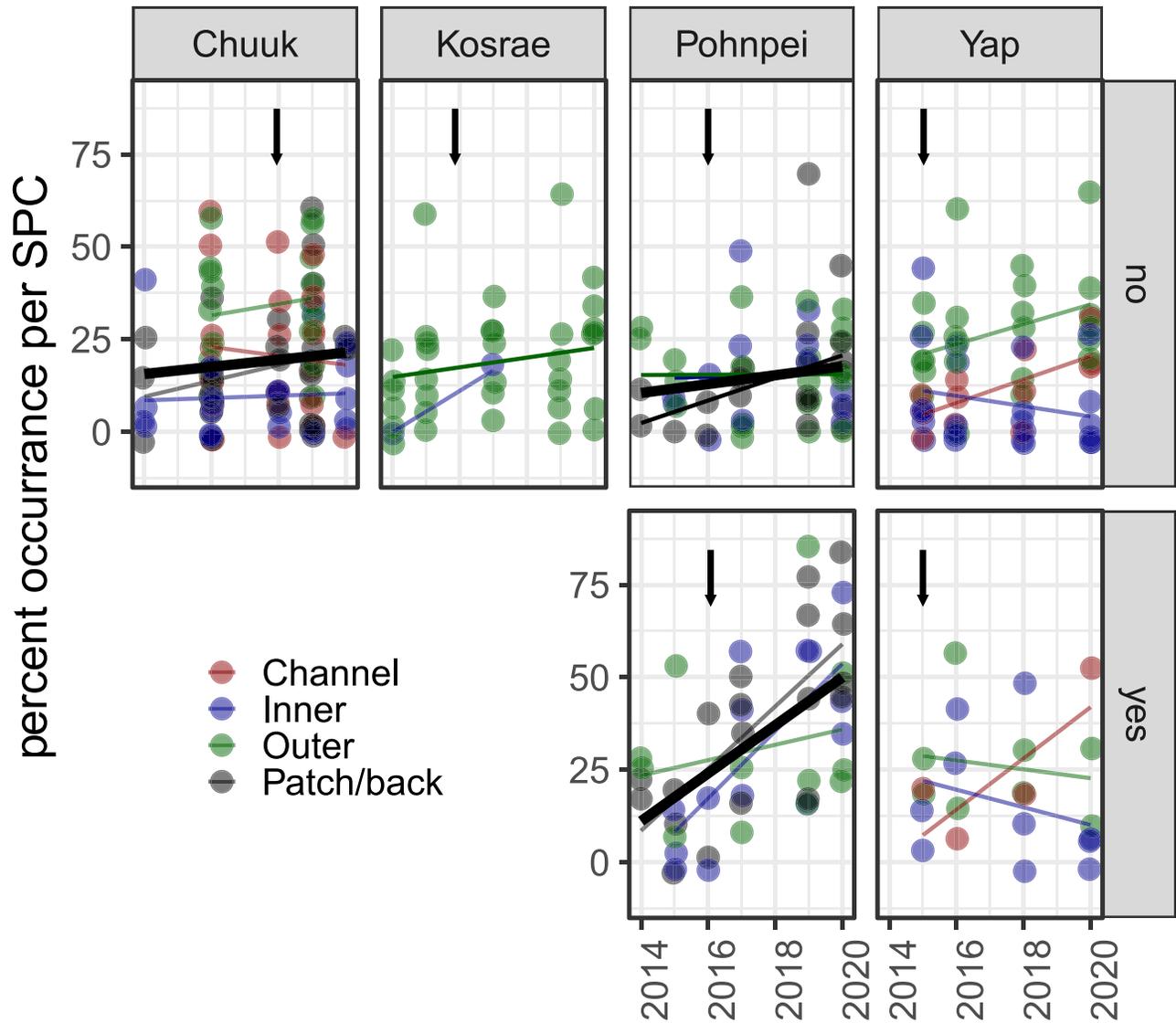


Fig 4. Trends in the occurrences of large groupers documented in spatially-restricted stationary-point-count surveys, with each point representing a site-year. Solid black lines indicate significant trends for the global model including all reef types, while colors indicate varying reef types. Methods describe how large grouper counts were comprised mainly of *Plectropomus areolatus* (~70%), with sparse contributions from other large grouper species. Black arrows indicate the timing of mass coral bleaching disturbances.

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data were also not influenced by MPA status. Meanwhile, Napoleon wrasse occurrences declined in Chuuk with no other island trends evident.

Spatially-unrestricted data were used to compare historical presence/absence data from the mid- 2000’s with modern data collected in 2020 for bumphead parrotfish and Napoleon wrasse on Yap and Pohnpei. These data suggested that site-level occurrences of bumphead parrotfish may have doubled through time, with MPA having a non-significant effect, and Yap having more observations compared to Pohnpei (Fig 6, complete convergence of model). Napoleon wrasse observations may have increased within modern MPA networks on Yap and Pohnpei, especially among inner reefs where juveniles are known to exist, but no similar increases were observed for non-MPA reefs, and no differences between the islands.

Table 1. Summary statistics for best-fit Bayesian models predicting site-level occurrences for three large targeted fish with active management based upon spatially-restricted survey observations.

	estimate	error	l-95%	u-95%	Rhat
<i>Cheilinus undulatus</i>					
time:Chuuk	-0.18	0.08	-0.34	-0.03	1.00
time:Kosrae	-0.04	0.08	-0.20	0.12	1.00
time:Pohnpei	0.09	0.07	-0.05	0.22	1.00
time:Yap	0.09	0.08	-0.06	0.24	1.00
<i>Bolbometopon muricatum</i>					
time:Chuuk	-0.52	0.24	-1.07	-0.11	1.00
time:Kosrae	0.03	0.14	-0.27	0.29	1.00
time:Pohnpei	0.13	0.09	-0.05	0.32	1.00
time:Yap	0.31	0.10	0.13	0.51	1.00
<i>Sharks</i>					
time:Chuuk	0.25	0.09	0.08	0.42	1.00
time:Kosrae	-0.41	0.25	-0.99	-0.02	1.00
time:Pohnpei	0.20	0.08	0.04	0.36	1.00
time:Yap	-0.42	0.19	-0.81	-0.10	1.00

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Discussion

Novel interactions between fisheries management policies and the responses of fish assemblages following climate change disturbance events were found. We estimated a doubling of fish biomass on all study islands one year following disturbances suggesting MPA may not bolster fish responses. Instead, responses were associated with bottom-up pulses of algae and detritus following disturbances that support increased fish growth [44], recruitment, and survival [17]. However, longer durations of increased fish biomass at the island scale coincided with the presence and effectiveness of MPA. Fluctuations in fish biomass following disturbances have been observed by some long-term monitoring programs and defined in modeling studies. For instance, modeling studies in our study region highlighted the benefits of cyclical feedback loops between fish and coral-algae dynamics following disturbances [19], however, fewer studies have followed these feedback cycles across both disturbances *and* fisheries management regimes to draw comparisons with [26, 27, 45].

A study from Seychelles found that both MPA and fished reefs had slightly lower fish biomass 7 years after a 1998 mass coral bleaching event compared to a 1994 baseline, and that well-enforced MPA did not improve fish or coral recovery between 2005 and 2014 compared to reference reefs [26]. Meanwhile, MPA in Kenya maintained higher herbivore biomass compared to reference reefs before and after the 1998 mass bleaching, but slower recovery to pre-disturbance coral states in MPA were likely a consequence of greater cover and diversity in protected areas [27]. Given that coral-fish feedback loops are expected to be dynamic with peaks and troughs following disturbances [19], survey timing and management are expected to have complex interactions that may not be well understood yet leading to differing conclusions. We reported peak fish biomass 1 to 4 years following the disturbance on Pohnpei, where the most effective MPA network existed, but increased fish biomass only lasted 1 to 2 years elsewhere. These findings resonated with remote reefs in western Australia where peak density of herbivores remained evident 3 to 4 years following bleaching with a gradual decline to pre-disturbance levels by year 6 or 7 when coral recovery was close to pre-disturbance states [17]. Therefore, effective MPA networks appeared to modulate climate change disturbances in our region by extending the length of time that increased fish biomass was evident following mass coral bleaching. In support, the duration of increased fish size structures and densities differed

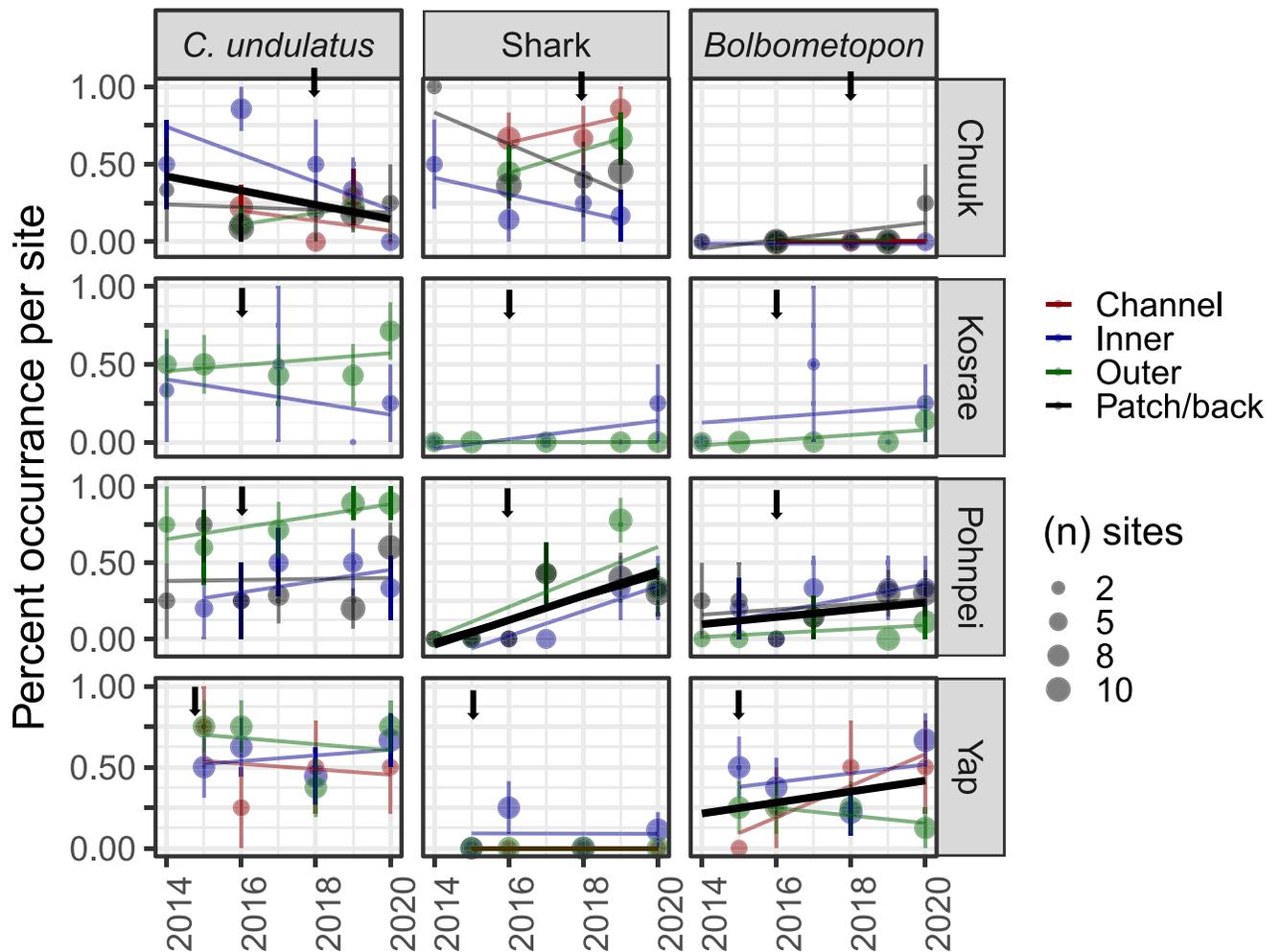


Fig 5. Trends in the occurrences of Napoleon wrasse, sharks, and bumphead parrotfish documented in spatially-restricted stationary-point-count surveys, with each point representing a reef type-year, with point size scaled by the number of survey reefs (n). Solid black lines indicate the presence of overall trend across reef types, colors highlight all reef type trends. Black arrows indicate disturbances.

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between MPA and non-MPA reefs suggesting that fishing pressure diminished the frequency, but not amplitude, of feedback loops.

Many fisheries management recommendations are based upon the maintenance or enhancement of biomass for individual species, trophic-levels, or entire fish assemblages [46, 47]. However, as climate change disturbance increase in intensity and/or frequency, our results predicts that biomass estimates will become more variable and dependent upon disturbance cycles. Therefore, we had to evaluate biomass targets while considering both the timing of disturbance cycles and reference sites/islands that control for management regimes. The results suggested that biomass-based management objectives should focus on maximizing the length of time fish biomass increases will remain evident following climate change disturbances. This could be accomplished through temporary policies protecting species, sizes, or areas, and would serve to facilitate resilience to the extent possible given local conditions. Further, past and present research suggested that fish responses lasted 4 to 5 years, providing a timeframe to consider alongside proactive climate-disturbance policies.

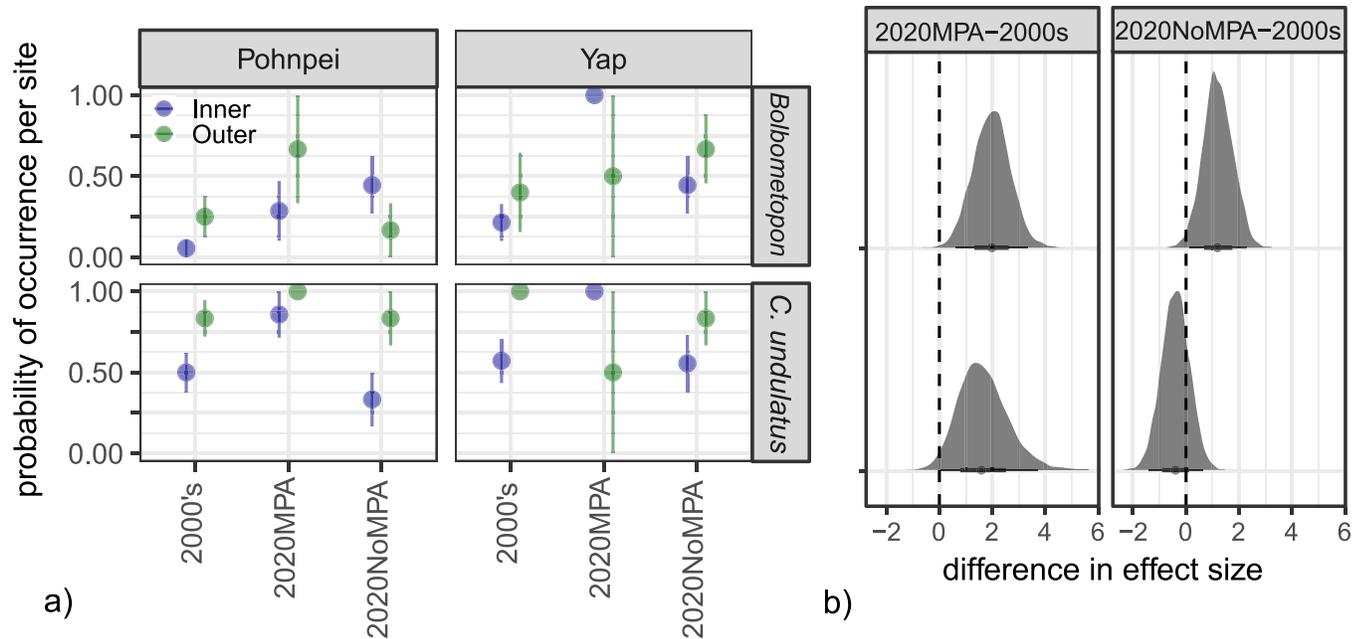


Fig 6. Trends (a) and contrasts of posterior Bayesian estimates (b) for two large targeted fish based upon spatially-unrestricted observations: Napoleon wrasse (blue) and bumphead parrotfish (green). Contrasts between presence/absence data from rapid ecological assessments conducted in the mid-2000's and the present 2020 surveys are shown for MPA (a) and non-MPA (b) reefs.

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Large targeted species differed markedly in terms of their temporal trends and interactions with MPA. Spatially-restrictive surveys suggested that management policies have led to clear improvements for groupers and minor improvements for bumphead parrotfish and sharks, while spatially-unrestrictive surveys revealed improvements for bumphead parrotfish over the past two decades. However, management policies were initiated before disturbances in most cases. Therefore, increasing trends may have been confounded with disturbance responses, but three conclusions were clear. First, MPA and species-based policies had synergistic interactions for groupers, which were dominated by *Plectropomus areolatus* that have a relatively small home range compared to body size [48], as annual increases were 2 to 3 times higher in MPA. This suggested protection of spawning aggregations has benefitted grouper populations. Second, sharks and bumphead parrotfishes with larger home ranges had greatest increases on Pohnpei, where the network of MPA was largest and most effective. Thus, individual MPA did not appear to benefit these large targeted species, however, a network of MPA may have. Third, potential increases for bumphead parrotfish and Napoleon wrasse over the past two decades were most notable across inner reef MPA where juveniles with small home ranges are known to prefer. These species are highly vulnerable across the Pacific and were among the first to be harvested unsustainably for commercial purposes [3, 49].

We summarize that most large targeted species have benefitted from management policies, however, the rates of increase were modest and based on probability of occurrences at the site level. Comparisons with remote Pacific reefs with little human influence highlight biomass differences that are orders of magnitude apart from our study islands [50, 51], indicating that management targets might be derived based upon unfished reference points. Coupled with our rates of increase, managers can begin to predict the time needed to reach their targets and evaluate if policies need to evolve further.

Conclusions

Growing commercialization of coral-reef fisheries have created the need for simplified management policies that often stem from traditional tenure systems, such as no-take MPA and full bans on species and spawning events. We report the success of these policies for improving fisheries across Micronesia during the past decade, but caution that interactions with climate-induced disturbance cycles may have exaggerated their perceived success. We further revealed synergies between MPA and species policies that suggested MPA networks represent a foundation upon which other policies can benefit from. Last, we recommend temporary policies to sustain feedback loops between benthic substrates and fish assemblages as disturbance events become more frequent and climate change intensifies.

Supporting information

S1 Table. Marine protected area attributes for Pohnpei and Yap Islands, Federated States of Micronesia.

(DOCX)

S2 Table. Species based policies established within the Federated States of Micronesia study islands.

(DOCX)

S1 Fig. Trends in non-coral calcifying versus non-calcifying substrates (a) and coral cover (b) across the study islands exposed to the their most recent disturbance event that was investigated in the present study (red arrows). The most dominant non-coral, calcifying substrates that were impacted by disturbances included crustose coralline algae and soft corals to a lesser extent (a, blue color). The most dominant non-calcifying substrates that responded to temperature stress events included turf and macroalgae, as well as cyanobacteria and encrusting red/brown algae with little calcification (i.e., *Lobophora* and some species within *Peyssonneliaceae*) (a, brown color). Coral cover data along the same disturbance timeline showing trends for four major coral groups (b) (*Acroporidae*, *Poritidae*, *Merulinidae*, and all other corals grouped). Data were derived from benthic photo quadrats taken along replicate 50m transects noted in the methods. Together, these graphs highlight the loss of coral and/or calcifying substrates associated with the most recent thermal stress event, and the replacement with non-calcifying substrates. In turn, these trends were associated with fish assemblage responses reported in the results.

(DOCX)

S2 Fig. Size-structure (a) and abundance (b) of Micronesia fish assemblages in the year before, 1-year after, and 3-years after a mass coral bleaching event. Trends are shown for both MPA and non-MPA reefs open for fishing.

(DOCX)

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