Biological Conservation 269 (2022) 109546

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

External fishing effort regulates positive effects of no-take marine protected areas

Shelby L. Ziegler [a,*], Rachel O. Brooks [a], Scott L. Hamilton [a], Benjamin I. Ruttenberg [b], Jennifer A. Chiu [a], Ryan T. Fields [c], Grant T. Waltz [b], Chenchen Shen [d], Dean E. Wendt [b], Richard M. Starr [a]

[a] Moss Landing Marine Laboratories, San Jose State University, 8272 Moss Landing Road, Moss Landing, CA 95039, USA
[b] Center for Coastal Marine Sciences, Biological Sciences Department, California Polytechnic State University, San Luis Obispo, CA 93407, USA
[c] Oregon Department of Fish and Wildlife, Marine Resources Program, 2040 Southeast Marine Science Drive, Newport, OR 97365, USA
[d] Marine Protected Areas Management Project, California Department of Fish and Wildlife, 1123 Industrial Road, Suite 300, San Carlos, CA 94070, USA

ARTICLE INFO

Keywords:
Marine reserves
Anthropogenic stressors
Environmental conditions
Fisheries
Community-based science
Socio-ecological interactions

ABSTRACT

Marine protected areas (MPAs) have been established across the globe to mitigate the effects of multiple stressors on marine communities. In many locations, MPAs have generated positive effects on fish communities, but the impacts of fishing pressure—the primary stressor MPAs seek to manage—have not been well investigated. We examined changes in fish biomass inside and outside of no-take MPAs over 14 years in central California, USA. Using data from the community-based science program, the California Collaborative Fisheries Research Program, we tested which environmental and human-induced stressors most influence the strength of MPA responses. While temperature and productivity were included in the best fit model, we found that fine-scale fishing effort data, following reserve implementation, best explained the spatial variation in fish community responses to MPAs. Specifically, differences in fish biomass between MPAs and sites open to fishing were larger for reserves near heavily fished locations and these areas exhibited the highest rate of change in fish biomass, indicating strong positive effects of the MPA on the most heavily exploited fish communities. As MPAs continue to be used as a prominent conservation strategy in coastal systems, managers should consider both the suite of human-induced (socio-ecological interactions) and environmental conditions that may alter MPA success as well as establish long-term monitoring programs to fully assess the functionality of marine reserves into the future.

1. Introduction

Anthropogenic stressors including overfishing, pollution, and climatic change threaten coastal ecosystems across the globe and have resulted in the decline of important fishery species (Lotze et al., 2006, 2018; Worm et al., 2006, 2009). To mitigate the effects of these stressors—and especially that of fishing—marine protected areas (MPAs) have been implemented to enhance overall biodiversity and maintain healthy coastal ecosystems (Micheli et al., 2012). Extensive research on MPAs has consistently shown that the biomass, abundance, diversity, and body size of marine species typically increase within no-take marine reserves (Guidetti et al., 2014; Lester et al., 2009). However, the strength and outcome of these MPA effects have been correlated with a variety of parameters (Caselle et al., 2015; Edgar et al., 2014; Gill et al., 2017; Knott et al., 2021) and are highly context-dependent, varying across both space and time.

Understanding which factors influence the strength and rate of MPA responses is important for adaptive management and setting appropriate expectations for stakeholders who may be affected by reserve implementation. Modeling work has suggested that the responses of fish communities to MPAs should be related to MPA size, fish movements and rates of spillover, time since protection, environmental conditions, as well as fishing effort or intensity (Moffitt et al., 2013; Nickols et al., 2019). Importantly, empirical work has found support for many of these factors (Bosch et al., 2021; Goetze et al., 2021). Since no-take marine reserves restrict fishing, pre-existing and subsequent post-implementation fishing pressure adjacent to reserves should strongly influence the MPA response. Still, many models of MPA efficacy assume that fishing pressure is homogenous across an area, often due to a lack of fine-scale data on the spatial distribution of effort (Lynch, 2006). However, even across relatively small spatial scales, the influence of MPAs on their associated fish communities can vary substantially. For

* Corresponding author at: Odum School of Ecology, University of Georgia, 140 E Green Street, Athens, GA 30602, USA.
E-mail address: shelbylziegler@gmail.com (S.L. Ziegler).

https://doi.org/10.1016/j.biocon.2022.109546
Received 30 December 2021; Received in revised form 28 March 2022; Accepted 2 April 2022
Available online 21 April 2022

instance, Hamilton et al. (2010) found that differences in MPA responses across the Channel Islands, California (spanning ~100 km) were related to the geographic locations of reserves and local sea surface temperature. In addition, relatively few empirical studies have tested the effect of external fishing effort on the efficacy of MPAs (Lenihan et al., 2021). One empirical example examined the influence of pre-implementation fishing pressure on MPAs in southern California. The authors found that the difference in lengths of targeted fish species between MPAs and areas open to fishing were greater for MPAs which experienced higher fishing pressure prior to MPA implementation, compared to areas with lower fishing pressure (Jaco and Steele, 2020). Still, few studies have explored the community or ecosystem impacts of fishing pressure on MPA responses.

In 2007, California began a stakeholder driven process to implement a network of MPAs spanning the entire state coastline. The process utilized input from fishers, conservationists, and other stakeholders, as well as scientific recommendations on sizing and spacing that were informed by data on habitat, abundances of key indicator species, home range size, and estimates of larval dispersal distances (Saarman and Carr, 2013). Over the past 15 years, researchers have monitored California MPAs and sought to assess the efficacy of these protected areas for enhancing the abundance, biomass, and diversity of species targeted by fisheries across multiple habitat types (e.g., kelp forest, nearshore rock; Caselle et al., 2015; Starr et al., 2015).

The California Collaborative Fisheries Research Program (CCFRP) focuses on monitoring how nearshore rocky reef fishes respond to MPAs. CCFRP is a community-based research program and partnership of volunteer anglers, scientists, NGOs, Commercial Passenger Fishing Vessel (CPFV) charter businesses, and resource management agencies (California Department of Fish and Wildlife [CDFW] and NOAA National Marine Fisheries Service [NMFS]) interested in sustainable fisheries. By combining the expertise and ideas of these diverse groups, CCFRP has successfully established rigorous and standardized scientific-fishing protocols to monitor socioeconomically valuable fish species in MPAs relative to reference sites open to fishing (Wendt and Starr, 2009).

In this study, we utilized data from CCFRP to test spatial and temporal variability in targeted fish communities inside and outside of four no-take MPAs along the central coast of California from 2007 to 2020. Fine-scale estimates of fishing effort were derived from the CDFW California Recreational Fisheries Survey (CRFS). We also included high resolution quantitative data on environmental conditions (e.g., sea surface temperature, net primary production, wind speed, and wave energy). Sites included Año Nuevo State Marine Reserve (SMR), Point Lobos SMR, Piedras Blancas SMR, and Point Buchon SMR (Fig. 1). Specifically, we evaluated how total fish biomass changed after implementation of MPAs and what external forces drove changes in fish biomass through time. We hypothesized that MPAs would have an overall positive effect on fish biomass, but the magnitude of change would be mediated by environmental conditions and fishing pressure adjacent to reserves. We analyzed (1) 14 years of fishery-independent catch-and-release data, beginning the year of MPA implementation, (2) environmental data on oceanographic conditions, and (3) fishing effort data in our reference sites to test which factors influenced the strength of MPA responses of recreationally important nearshore fishes. We found that fine-scale fishing pressure explained the majority of variance in the fish biomass response between MPAs and sites open to fishing, providing the first clear empirical evidence of the importance of post-implementation fishing effort in affecting the strength of MPA

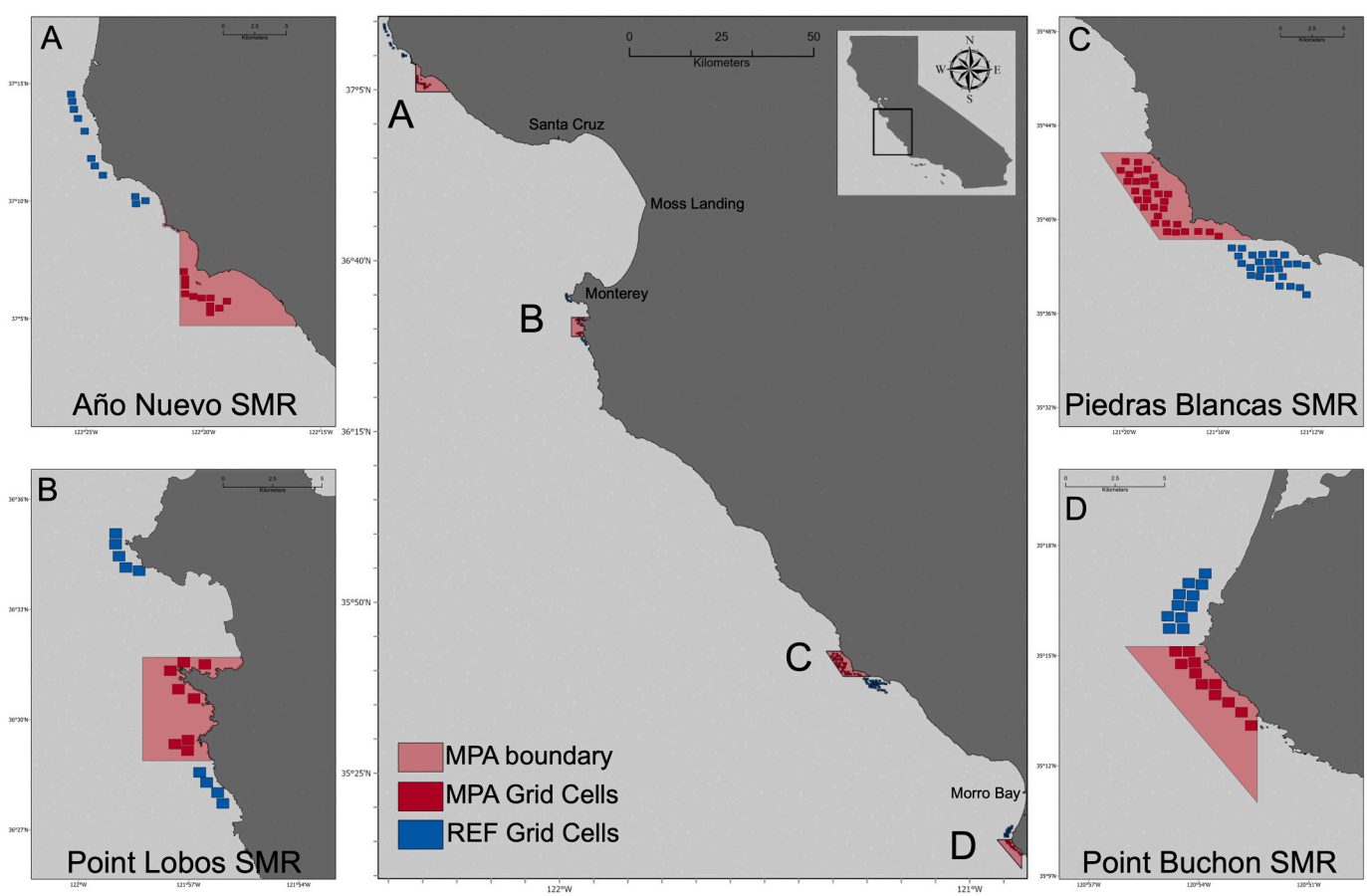

Fig. 1. Map of MPA and reference site (REF) sampling grid cells at (A) Año Nuevo, (B) Point Lobos, (C) Piedras Blancas, and (D) Point Buchon State Marine Reserves. Shaded red area indicates MPA boundaries. MPA grid cells in red. REF grid cells in blue. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

responses.

2. Materials and methods

2.1. Fishery-independent CCFRP sampling

Sampling occurred in four different geographic locations along 350 km of coastline (Fig. 1). Each location contained one MPA and paired reference site (Wendt and Starr, 2009; Yochum et al., 2011). Sampling locations included four no-take State Marine Reserves where fishing is not permitted (Año Nuevo, Point Lobos, Piedras Blancas, and Point Buchon) and the reference sites associated with each of these MPAs. Corresponding reference sites were selected based on the criteria that they share similar habitat, bathymetry, and oceanographic conditions with the MPAs but are far enough away to minimize the potential that fish populations inside a reference site are greatly influenced by a nearby MPA (e.g., by adult spillover from the MPA to the reference site). Given those criteria, reference sites were located 0.5–10 km away from the corresponding MPAs. Collaborating anglers were helpful in choosing appropriate survey areas and reference sites for the MPAs by applying their extensive knowledge of the historic fishing activity and the available habitat at each site (Yochum et al., 2011).

The Año Nuevo, Point Lobos, Piedras Blancas, and Point Buchon SMRs encompass areas of 26.4 km^2, 14.0 km^2, 26.9 km^2, and 17.4 km^2, respectively and are all located adjacent to limited-take State Marine Conservation Areas. Within the boundaries of each MPA and reference site, 500 m by 500 m fixed grid cells were delineated in rocky habitats shallower than 40 m depth (to limit fishing mortality associated with barotrauma). A total of 22 fixed grid cells at Año Nuevo, 17 cells at Point Lobos, 57 cells at Piedras Blancas, and 22 cells at Point Buchon (across MPAs and reference sites) were designated, numbered, and then chosen at random to be sampled on a given day (Fig. 1). Differences in the number of sampling cells reflect different sizes of the MPAs and amounts of suitable rocky habitat in the appropriate depth zones for sampling.

Surveys were conducted annually in the four areas from 2007 to 2020 (except that surveys did not occur at Piedras Blancas in 2007 and 2015). Volunteer anglers were recruited from various fishing clubs, online fishing websites, and from previous collaborative studies. Surveys occurred in the late summer period from mid-July through September, when ocean conditions in the region are most consistent. Each MPA or reference site was sampled at least six days per year. Before each day of fishing, four grid cells in a given MPA or reference site were randomly chosen for sampling. Captains were instructed to locate three suitable fishing locations within each grid cell to complete fishing drifts with a goal of 15 min each. For each drift, information on the number of fishers, time spent fishing, location (GPS coordinates), depth (ft.), habitat relief, and other environmental variables were recorded. We used a standardized set of fishing gear (lead jigs, shrimp flies without bait, and shrimp flies with squid bait) in order to capture a variety of species and cover the spectrum of typical hook-and-line fishing gear used in this region. Captured fishes were identified to species, measured to the nearest cm, and released. Lengths reported are total length, defined as the distance from the tip of the snout to the most posterior part of the caudal fin without compressing the tail. We recorded the locations (latitude and longitude) and depths where fishes were released. The effects of barotrauma were reduced with descending devices and by minimizing the duration of time that the fishes were on board the vessel. We aimed to process and release fish in <5 min in order to minimize effects of barotrauma and handling stress (Jarvis and Lowe, 2008).

2.2. BPUE and response ratio calculations

To standardize our sampling effort, we calculated biomass per unit effort (BPUE). BPUE was calculated as the total weight of fish in kilograms divided by the number of hours fished by anglers (kg angler h^{-1}) for each MPA and reference site. We first calculated BPUE for each fish caught by converting total length (cm) to weight (kg) using published length-weight relationships for each species (Love et al., 1990) divided by total time fished for each grid cell. BPUE for each grid cell sampled on a given day was averaged to estimate BPUE for the total fish community inside and outside each MPA in a given year of sampling. Using BPUE values, a yearly biomass response ratio was calculated to estimate the strength of the MPA effect on fish BPUE inside relative to outside the MPA. BPUE response ratios were calculated by taking the log of the quotient between biomass inside relative to outside the MPA: Log ($BPUE_{MPA}/BPUE_{Reference}$).

A biomass response ratio above zero indicates higher total fish biomass inside the MPA compared to the reference site, while a value below zero indicates higher total fish biomass in the reference site compared to the MPA.

2.3. Environmental data extraction

Environmental data (sea surface temperature, net primary production, wind speed, wave height and wave orbital velocity) were extracted from the Central and Northern California Ocean Observing System (CenCOOS) Repository (cencoos.org). Sea surface temperature (°C; SST) was originally collected from the Advanced Very High-Resolution Radiometer instrument aboard NOAA's Polar Operational Environmental Satellites. SST measurements were collected daily from 2004 to 2020 at a 1.47 km spatial resolution. Values are accurate to ±0.7 °C. Net Primary Production data (mg C m^{-2} day^{-1}; NPP) were collected by the California Current Merged Satellite daily from 1996 to 2020 at a 4 km spatial resolution. Wind Speed (m s^{-1}) was extracted from the Coupled Ocean/Atmosphere Mesoscale Prediction System (COAMPS) through the CenCOOS repository. COAMPS is a high-resolution meteorological forecast model with a 4-km resolution. Significant wave height (m) and wave orbital velocity (m s^{-1}; derived from wave height and dominant period) were extracted from the Coastal Data Information Program spectral files at the station nearest each MPA. Wind speed and wave metrics may affect underwater visibility, the presence of certain fish species due to increased turbulence, or could affect fishing quality and therefore were considered in modeling efforts. For all environmental variables, we extracted the mean monthly data for each CCFRP grid cell for the time period during sampling between the months of July and October from 2007 to 2020.

2.4. Fishery-dependent microblock data

Fishing effort data were obtained from the California Recreational Fisheries Survey (CRFS) conducted by CDFW from 2012 to 2019. We focused our efforts on the CRFS Private and Rental Boat (PR) surveys. These surveys are conducted by CRFS samplers at public launch ramps or access sites as anglers return from their fishing trips. The surveys are voluntary and anglers are interviewed about their fishing trips, including the number of people who fished, the number of days fished, the taxon targeted, and the catch location. CRFS data are spatially referenced across 18.52 km × 18.52 km (10 × 10 nautical mile) fishing blocks, which are further divided into 1.85 km × 1.85 km (1 × 1 nautical mile) fine-scale microblocks. We only used data that were reported at the finer microblock resolution. Although CRFS also collects information on catch, we focused on fishing effort, approximated by the number of angler days for each unique fishing trip. We extracted fishing effort data from the microblocks overlapping with each CCFRP reference site cell for each MPA and year available. The total number of angler days per year within a microblock were summed and then averaged across all microblocks for a given year and MPA area.

2.5. Statistical analysis

To assess total fish biomass in the MPA and reference sites with time since MPA implementation, we ran a two-way interactive Analysis of

Covariance (ANCOVA). To further assess the relative effect of protection (or fishing closure) on fish biomass from MPA implementation in 2007 to 2020, we ran generalized linear models on the calculated biomass response ratios through time at each MPA, independently. To determine if human-induced stressors (i.e., fishing pressure) and environmental conditions significantly varied across years and MPAs, we serially conducted linear models for each environmental variable and external fishing effort, independently, for years with sufficient data. Environmental data that differed statistically by year and location (sea surface temperature and primary production) were included while variables that were not significant (wind speed, wave height and wave orbital velocity) were dropped from subsequent analyses. To determine the relative influence of environmental conditions (sea surface temperature and primary production) and fishing effort on spatial differences in biomass response ratios (i.e., MPA effect size), we ran generalized additive mixed models (GAMM) with the mgcv package in R (Wood, 2011) to smooth the interannual stochasticity in the data. Our models included net primary production, mean sea surface temperature during the sampling period, and the number of angler days per microblock as fixed effects, with a smoothed random effect of year. The model with the best fit was selected using Akaike Information Criterion (AIC). All analyses were conducted in R statistical software version 4.0.5 (R Core Team, 2021).

3. Results

Fish BPUE (biomass per unit effort) increased in both MPA and reference sites from the time of MPA implementation at all sampling sites (Fig. 2). Overall, BPUE increased by 306% inside MPAs, while it increased on average by 80% in the reference sites. However, fish BPUE as well as the difference in fish BPUE between the MPA and reference sites varied by location and across years. Año Nuevo sampling sites contained the lowest fish BPUE compared to all other areas with a maximum annual mean BPUE of 9.8 kg angler h^{-1} (95% CI 8.9, 10.6).

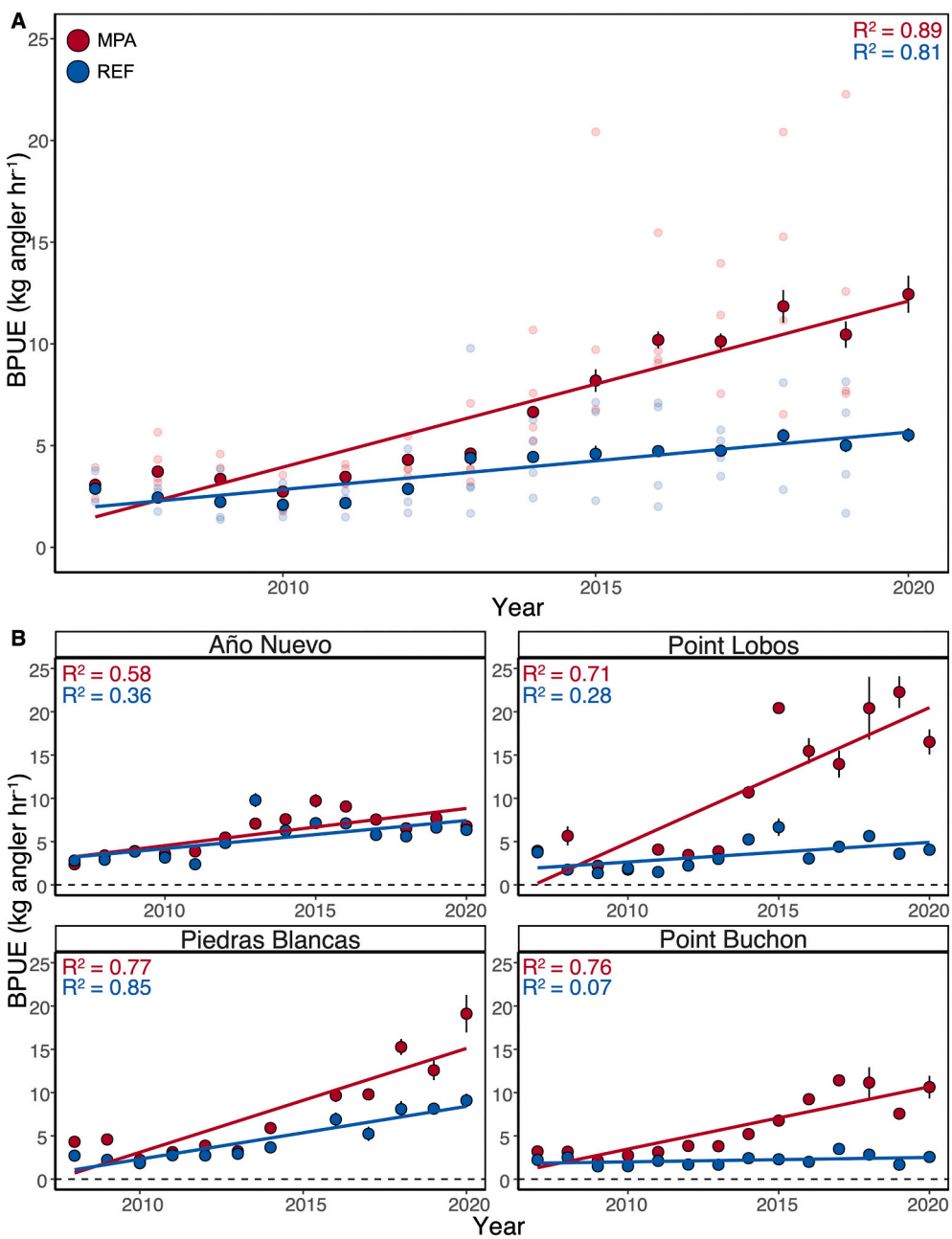

Fig. 2. Annual fish biomass per unit effort (BPUE) inside and outside of (A) 4 MPAs combined (faded points are individual MPA values and opaque points are means of the 4 central coasts MPAs) and (B) each of the 4 MPAs along the central coast of California. Red points are MPA sites and blue points are reference (REF) sites. Trend lines are linear regressions for the effect of time since implementation (year) on fish biomass. All values are means ± 95% CI. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Maximum annual mean BPUE was highest at Point Lobos at 22.3 kg angler h^{-1} (95% CI 20.4, 24.1). At Point Lobos, Piedras Blancas, and Point Buchon there was a significant interaction between year and protection status (MPA vs. reference) on changes in fish BPUE (ANCOVA: Year x Protection Status, Point Lobos: $F_{1,24} = 21.8$ $p < 0.001$; Piedras Blancas: $F_{1,24} = 7.92$, $p = 0.011$; Point Buchon: $F_{1,24} = 33.6$, $p < 0.001$, respectively), with BPUE increasing more rapidly inside the MPA at all three locations. At Point Lobos, BPUE increased by 320% inside the MPAs and by 8% in the reference site. At Piedras Blancas, BPUE increased by 432% inside the MPA and by 235% outside the MPA, while at Point Buchon, BPUE increased by 232% inside the MPA but stayed relatively constant (14% increase) in the reference site. At Año Nuevo, there was a significant increase in total fish BPUE over time (ANCOVA: Year, $F_{1,24} = 25.8$, $p < 0.001$), but no difference in the rate of BPUE accumulation between MPA and reference sites (MPA = ANCOVA: Year × Protection Status, $F_{1,24} = 1.42$, $p = 0.24$). At Año Nuevo, BPUE increased by 183% inside the MPA and by 125% outside the MPA.

The effect of MPA fishing closures on fish BPUE (i.e., BPUE response ratio comparing biomass inside the MPA relative to the paired reference site) was positive (higher BPUE inside MPAs relative to references) for all years averaged across the four Central Coast MPAs surveyed. The magnitude of the effect of the fishing closure on fish BPUE increased with time since implementation (Linear Regression: $F_{1,12} = 32.98$, $p < 0.001$, $r^2 = 0.71$), indicating that BPUE was increasing at a faster rate inside MPAs compared to reference sites. However, the rate of change in BPUE response ratios varied across MPA locations (Fig. 3). BPUE response ratios were positive for all years post-MPA implementation at Point Lobos, Piedras Blancas, and Point Buchon, indicating higher fish BPUE in MPAs compared to associated reference sites. BPUE response ratios were positive at Año Nuevo for all years except 2007 (year of implementation, lnRR = −0.16) and 2013 (lnRR = −0.32), indicating that fish BPUE was higher in reference sites compared to MPAs in those two years. BPUE response ratios increased significantly from the date of MPA implementation at Point Lobos (Linear Regression: $F_{1,12} = 13.22$, p

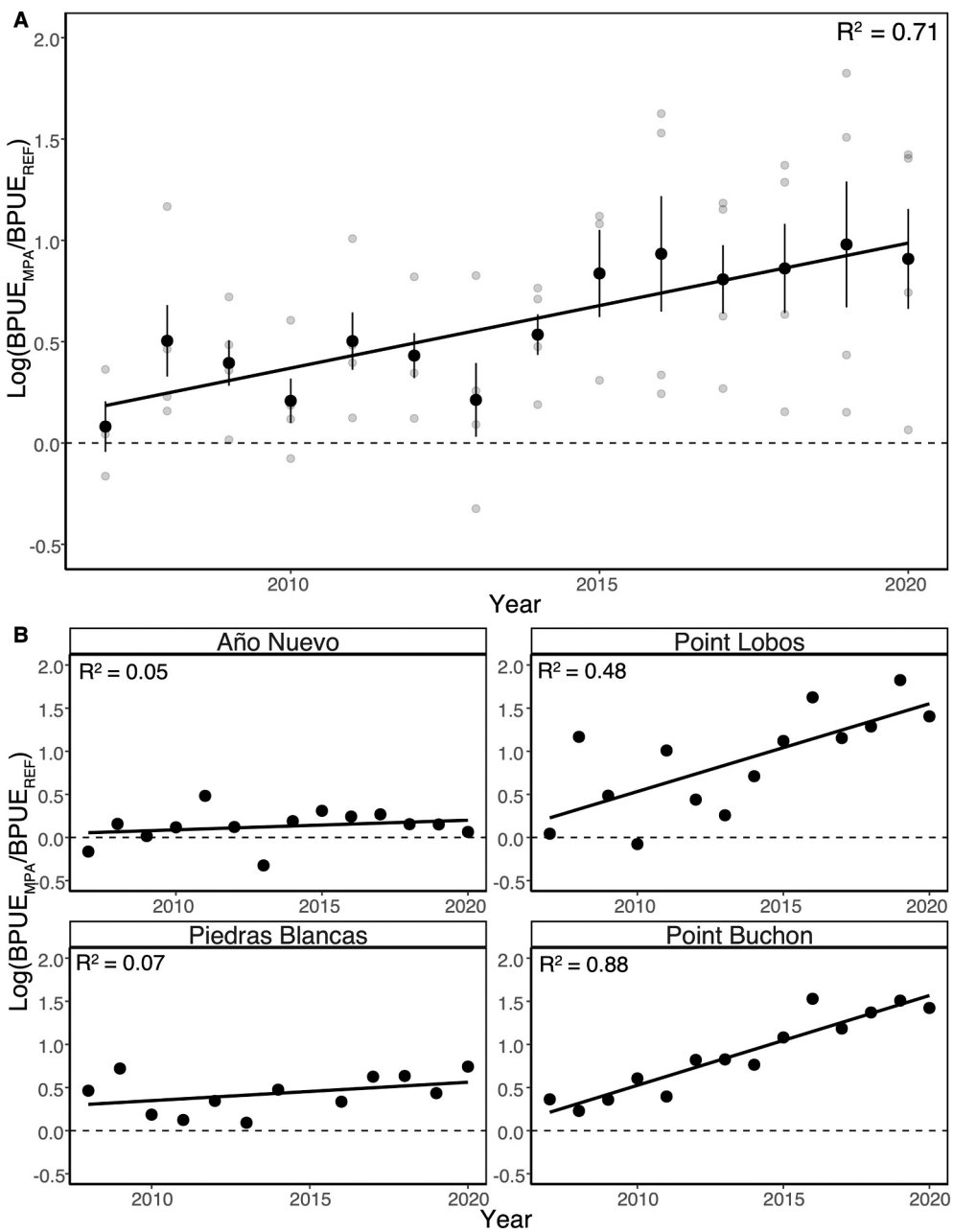

Fig. 3. BPUE response ratios for the (A) 4 MPAs combined (faded points are individual MPA values and opaque points are means of the 4 central coasts MPAs ± 95% CI) and (B) each of the 4 MPAs along the Central Coast of California from implementation in 2007 to 2020. Trend lines are linear regressions for the effect of time since implementation (Year) on biomass response ratios. BPUE response ratio values (y-axis) values greater than zero indicate higher total fish biomass inside the MPAs relative to the reference sites.

$= 0.003$, $r^2 = 0.52$) and Point Buchon (Linear Regression: $F_{1,12} = 96.41$, $p < 0.001$, $r^2 = 0.89$). At Año Nuevo and Piedras Blancas, BPUE response ratios slightly increased from the date of MPA implementation to 2020; however, these relationships were not statistically different (Linear Regression: Año Nuevo: $F_{1,12} = 0.71$, $p = 0.41$, $r^2 = 0.06$; Piedras Blancas: $F_{1,12} = 1.77$, $p = 0.21$, $r^2 = 0.15$; Fig. 3).

We identified clear differences in environmental conditions and recreational fishing effort among sites and with time since MPA implementation (Fig. A1). On average, mean sea surface temperature (°C) during the CCFRP sampling period ranged from ~13 °C to 17.5 °C and increased through time with peak temperatures at all sites occurring during a marine heatwave in 2014–2016 (ANOVA: $F_{1,43} = 7.80$, $p = 0.007$). Temperatures were highest in the southernmost location, Point Buchon, for all years sampled (ANOVA: $F_{3,43} = 3.83$, $p = 0.02$) compared to other MPAs (Fig. A2). Net primary production (mg C m^{-2} yr^{-1}) was also variable across years (ANOVA: $F_{1,43} = 4.03$, $p = 0.05$), ranging from 1000 mg C m^{-2} yr^{-1} to upwards of 3000 mg C m^{-2} yr^{-1} across MPA sites in a single year (ANOVA: $F_{3,43} = 7.64$, $p < 0.001$) (Fig. A3). Fine-scale recreational fishing effort extracted from CDFW microblocks (1.85 km × 1.85 km) from 2012 to 2019 showed high variability across years (ANOVA: $F_{1,23} = 6.8$, $p = 0.015$) and sites adjacent to MPAs (ANOVA: $F_{3,23} = 52.57$, $p < 0.001$). Reference sites outside of Point Lobos and Point Buchon had 2–3× as many angler days per microblock as Piedras Blancas or Año Nuevo in a given year (Fig. A4). We also examined wind speed, wave height and wave orbital velocity and found them to be non-informative, so excluded them from the final models.

Fine-scale recreational fishing effort and time since MPA implementation showed a clear influence on BPUE response ratios. This indicates that the differences in fish BPUE between the MPA and reference sites depend on the level of fishing pressure outside the MPA in a given year (Table 1; Fig. 4). The trends in BPUE were dominated by the top ten most abundant species at our sites (Fig. A5), with species such as the blue and deacon rockfish complex (*Sebastes mystinus* and *Sebastes diaconus*), olive rockfish (*Sebastes serranoides*), gopher rockfish (*Sebastes carnatus*), copper rockfish (*Sebastes caurinus*), vermilion rockfish (*Sebastes miniatus*), and lingcod (*Ophiodon elongatus*) contributing most to the differences in BPUE between MPA and reference sites. The best fit GAMM model, identified by model selection with AIC, included fine-scale fishing effort, smoothed terms for sea surface temperature and net primary production, and a random effect of time since MPA implementation (GAMM: $r^2_{adj} = 0.67$; Table 1). Fishing pressure post-implementation was the single most important variable in explaining spatial and temporal variation in biomass response ratios across all sites, accounting for 71.9% of the deviance alone (Table 2). Specifically, there was a clear positive relationship between external fishing effort in a given year and BPUE response ratios (GAMM: $t = 5.58$, $p < 0.001$), whereby the strongest MPA responses (i.e., differences between fished and unfished sites) occurred in locations with the highest fishing effort outside the MPA (Table 2). A random effect of time since MPA implementation also had a clear positive association with biomass response ratios (GAMM: $F = 10.02$, $p = 0.002$) indicating that the longer the MPA is in place, the larger the differences in BPUE between MPAs and reference sites, regardless of the amount of external fishing effort. Smoothed temperature and net primary production values were included in the model as predictors of biomass response ratios (based on model selection via AIC). However, net primary production had a small negative association with BPUE response ratios (GAMM: $F = 4.71$, $p = 0.04$) and there was no association between temperature and BPUE response ratios (GAMM: $F = 0.86$, $p = 0.46$).

Table 1
Comparison of generalized additive mixed model predicting the influence of fishing effort and environmental variables (SST and NPP) on fish biomass response ratios at four central California MPAs.

Model	df	AIC
Sea surface temperature + s(1|Time since implementation)	3.866	47.937
Primary production + s(1|Time since implementation)	3.883	45.505
Fishing effort + Sea surface temperature + s(1|Time since implementation)	4.890	26.693
Fishing effort + s(Sea surface temperature) + s(1|Time since implementation)	5.229	26.387
Fishing effort + s(1|Time since implementation)	3.899	24.765
Fishing effort + Sea surface temperature + s(Primary production) + s(1|Time since implementation)	5.915	23.847
Fishing effort + Sea surface temperature + Primary production+ s(1|Time since implementation)	5.916	23.847
Fishing effort + s(Sea surface temperature) + s(Primary production) + s(1|Time since implementation)	6.487	22.834

4. Discussion

The ecological success of MPAs will be dictated by a variety of environmental and human-induced factors (Edgar et al., 2014). We found that differences in the amount of total fish biomass inside MPAs, in comparison to external fished reference sites, were greatest in locations with high fishing pressure post-MPA implementation. Our results present the first empirical evidence that the responses of fish assemblages in MPAs are directly related to the amount of human-induced fishing pressure outside of a reserve following implementation, and that this response is mediated by the time since MPA implementation. Environmental conditions of water temperature and primary productivity explain additional variation in fish biomass responses, but their contributions were negligible compared to the effects of fishing pressure and MPA age. These findings provide empirical evidence that human activity – namely fishing pressure – following MPA implementation can influence the trajectory and time required to observe the benefits of reserves for key species and fish communities. Further, our study highlights the need for reliable information regarding human activity to help set expectations for what responses might occur following MPA implementation.

The Point Lobos and Point Buchon SMRs experienced the highest relative fishing effort outside the MPAs (50–150 angler days microblock^{-1} yr^{-1}) and exhibited the highest rate of change in BPUE response ratios. In both of these locations, fish BPUE increased steadily inside the MPA, while biomass stayed at a relatively constant level in the reference sites. Some researchers have expressed concern that MPAs may result in redistribution of fishing effort to remaining locations open to fishing; however, we found that the level of fishing effort in our study locations was not sufficient to depress fish populations in these reference sites (Agardy et al., 2011; Murawski et al., 2005). In contrast to previous MPA synthesis studies (Kellner et al., 2007; Ohayon et al., 2021), fishing pressure adjacent to MPAs in central California did not appear to slow growth of fish populations inside the MPAs themselves. Furthermore, the magnitude of BPUE response ratios at locations with high fishing effort increased with time since MPA implementation, indicating that the benefits from these MPAs are still accumulating, even 14 years after fishing was prohibited inside the MPA (Babcock et al., 2010; Nickols et al., 2019; Starr et al., 2015).

In contrast, at Piedras Blancas and Año Nuevo SMRs, sites with low relative fishing effort outside the MPA (<50 angler days microblock^{-1} yr^{-1}), there was a much weaker, and non-significant, positive increase in biomass response ratios since MPA implementation. At these two locations, fish BPUE increased through time in both the MPA and reference sites, potentially reflecting the effects of strong recruitment and year-class strength, or other fishery management actions, that were not erased by high fishing pressure outside the MPAs (da Silva et al., 2015; Jennings, 2000). While these sites are still showing benefits of fishing closure on fish communities, the positive effects are slower to accumulate (when comparing the MPA to their paired reference site) relative to MPAs near areas experiencing higher fishing effort. Previous studies have found that the amount of fishing pressure in an area prior to closure is one of the best indicators of MPA success for targeted fishes across tropical and temperate systems (Jaco and Steele, 2020; Lenihan et al.,

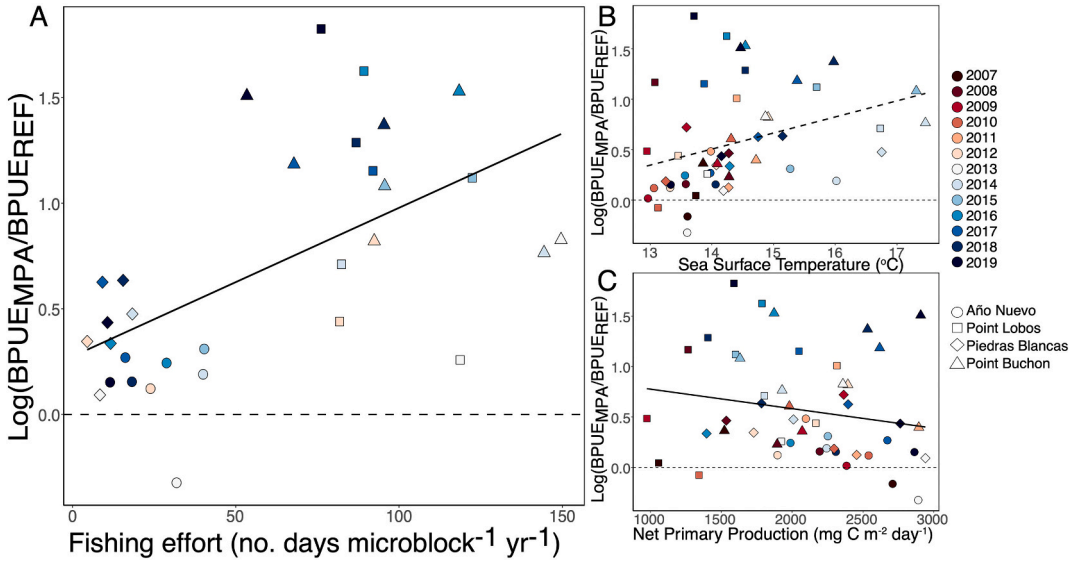

Fig. 4. Fishing effort (A) and environmental variables [SST (B) and NPP(C)] in relation to biomass response ratios for the 4 MPAs along the Central Coast for years with sufficient data between 2007 and 2019. Trend lines are linear regressions for the effect of each variable on BPUE response ratios. Solid regression lines indicate statistically significant relationships, dashed regression lines indicate non-significant relationships. BPUE response ratio values (y-axis) greater than zero indicate higher total fish biomass inside the MPAs relative to the reference sites.

Table 2
Output for the best fit model testing the influence of fishing effort and environmental variables on fish biomass response ratios at four central California MPAs.

Model output			
Predictors	Estimates	CI	*p*-Value
Intercept	0.214	−0.17–0.60	0.249
Fishing effort	0.011	0.009–0.013	<0.001
s(Sea surface temperature)			0.465
s(Primary production)			0.039
s(1|Time since implementation)			0.002
Observations	31		
R^2	0.669		

2021; Nillos Kleiven et al., 2019). Our study is the first to use empirical fishing effort data post-MPA implementation and indicates that after redistribution of fishing effort due to closure, the amount of fishing pressure in areas outside an MPA is the strongest predictor of fish responses to MPAs over time.

We propose that angler behavior and fine-scale fishing effort outside of an MPA post-implementation (i.e., adaptive human feedback; Champ et al., 2018), may be a better indicator of MPA efficacy through time for targeted fish communities than pre-implementation fishing pressure. For instance, the area now within Piedras Blancas SMR experienced historically high fishing pressure due to the presence of extensive high-quality fish habitat, even though this site was relatively far from port (California Ocean and Science Trust and California Department of Fish and Wildlife, 2013). The longer distance from port, requiring good weather days to reach, and a lower amount of high-quality fishing area available post-MPA implementation may have resulted in a decline in total fishing effort in the reference sites, rather than the expected redistribution of effort to locations directly outside the MPA (Ivens-Duran, 2014).

At both Piedras Blancas and Año Nuevo (where BPUE increased both inside and outside the MPAs after closure) the combination of distance from port and changes in angler behavior across years dampened fishing effort outside the MPA (similar to observations by Lynch, 2014). This resulted in a slower accumulation of perceived MPA benefits compared to locations with high fishing effort in the reference sites. Thus, low fishing effort outside the MPA resulted in similar rates of biomass increase both inside and outside the MPA. This phenomenon emphasizes the need to incorporate socio-ecological interactions (Pollnac et al., 2010) and the optimization of fisheries management into predictions and expectations of conservation outcomes, in addition to traditional metrics used in reserve network design (e.g., size, spacing, configuration, etc.; Gaines et al., 2010; Rassweiler et al., 2012). This is not to say MPAs should not be placed in areas with low relative fishing effort (especially within a reserve network), but more appropriately scientists and managers should expect a slower and less dramatic response of fish communities to MPA implementation in areas of low fishing pressure compared to areas with high fishing pressure.

The results of our study are dependent on the quality of fishing effort data provided by the CRFS and the locations of our survey sites. There may be variability in the proportion of anglers participating at each port and across years however, the average number of angler fishing days across microblocks and years clusters by the marine reserves sampled. For example, at Piedras Blancas angler days are consistently less than 25 days per year while at Point Buchon angler days are greater than 75 days across all years sampled (Fig. A1). These stark and consistent differences in relative fishing effort among locations increase our confidence in the reliability of the fine-scale fishing effort data from the central coast management region, at least in relative terms. The rank ordering of sites by fishing pressure from the CRFS data also match expectations based on conversations with anglers, fishing captains, and other experts in terms of which sites experience the highest and lowest fishing effort. Furthermore, inaccuracies or other noise in these fishing effort data would also be more likely to obscure any patterns we observed, such that our estimates of the impacts of fishing effort on MPA responses may be conservative.

Our best fit model also included environmental conditions such as sea surface temperature and net primary production, but these variables had negligible effects on BPUE response ratios (Fig. 4). This indicates that the extent to which environmental conditions will influence underlying annual variability in fish biomass within coastal systems seems to be independent of MPA protection status. Further evidence for this pattern comes from the marine heatwave that impacted the California coast between 2014 and 2016. This significant thermal anomaly impacted ecosystems across the state and also altered fish community composition of marine reserves (Freedman et al., 2020). While the

community composition within MPAs may have changed during this event, our results suggest that fish biomass changed similarly inside and outside of MPAs. Freedman et al. (2020) found that targeted species, which benefit the most from fishing closures, were least affected by the heatwave. Our data show that BPUE of recreationally targeted fishes inside the MPAs and biomass response ratios did not drastically decline during or after the marine heatwave, further supporting the observation that MPAs may mitigate the effects of temperature anomalies on the overall biomass of recreationally targeted coastal fish communities. However, the potentially minimal impact of temperature anomalies on targeted fishes may only hold true for temperate MPAs. In tropical systems, MPAs are dominated by coral reef systems where extreme temperature shifts appear to drastically impact overall reserve functionality (Graham et al., 2020). The impacts of temperature anomalies on tropical systems are exacerbated by coral bleaching and the loss of structured habitat. However, communities within temperate MPAs may be better able to withstand future climatic shifts due to higher resilience of habitat structure (i.e., rocky reefs vs. coral reefs; Brown et al., 2021; Reed et al., 2016). Alternatively, the lack of a clear influence of anomalous temperature on fish biomass within these temperate MPAs may be a result of our sampling across a section of coastline with a relatively small temperature gradient.

Primary production flows through an ecosystem and can directly contribute to increased biomass or secondary production in higher level consumers, such as fish communities. Our results show a small negative relationship between primary production and fish BPUE. This is most likely due to higher productivity occurring at the Año Nuevo SMR where BPUE response ratios and fishing effort were the lowest. Primary production in upwelling systems, such as the California coast, varies greatly both spatially and temporally (Checkley and Barth, 2009) and previous studies have shown these oscillations in productivity influence processes such as recruitment and year class strength, potentially explaining the negative relationship we observed (Caselle et al., 2010). Higher resolution primary productivity data or future considerations of lag effects from changing environmental conditions may assist in the development of predictive models for MPA efficacy through time (Barceló et al., 2021). The temporal variability in environmental conditions may have had a greater impact on fish communities closer to the time of MPA establishment (White et al., 2010, 2011) as previous studies have shown that along the central California coast there was no influence of MPAs on fish communities until more than five years post-implementation (Starr et al., 2015). In addition, across our sites, there may be potential for fishing naivete within the reserves to inflate catches relative to areas open to fishing (Alós et al., 2015). However, we would expect naivete to fishing to be consistent across all marine reserves and would not fully explain why we observed higher catches inside the MPA to continually increase through time. While temperature, productivity, and fish behavior may have had small effects on BPUE response ratios, our data strongly suggest that fishing pressure and reserve age are the dominant factors driving the intensity of the ecological responses of MPAs.

5. Conclusion

Overall, our study suggests that understanding fishing pressure is critical for planning and managing MPAs, and for setting realistic expectations from those MPAs. Specifically, the placement of reserves in areas with low fishing pressure may protect fish assemblages, but those areas will experience slower community-level responses to fishing closure. MPAs placed in areas of high fishing pressure are more likely to show faster recovery (Edgar et al., 2014; Pressey, 1994). In addition, predicted future fishing pressure outside an MPA can also help set expectations in MPA planning and development. Metrics such as distance from port, or the amount of high-quality fish habitat surrounding an MPA may provide a more comprehensive prediction of the outcomes of these conservation tools. Lastly, our study further supports the concept that MPAs are long-term conservation tools with full effects that may not be realized until 10 years or more post implementation, particularly in temperate systems (Addison et al., 2015; Heupel and Simpfendorfer, 2005; Ojeda-Martinez et al., 2007; Smale et al., 2019). As MPAs continue to be used as a prominent conservation strategy in coastal systems, managers should consider both the suite of human-induced (socio-ecological interactions) and environmental conditions that may alter MPA success as well as establish long-term monitoring programs to fully assess the functionality of marine reserves into the future.

Data availability

Data used in this manuscript are publicly available in the California Ocean Protection Council DataONE portal: Starr et al. (2021). Nearshore Fishes Abundance and Distribution Data, California Collaborative Fisheries Research Program (CCFRP), 2007–2020. California Ocean Protection Council Data Repository. doi:10.25494/P6901R. All code for data analysis can be found at https://github.com/slziegler/CCFRPMicroblockAnalyses.

Ethical approval

IACUC protocols (SJSU IACUC #824, #1021). CDFW Scientific Collecting Permit #2613, S-191210002-19126-001.

CRediT authorship contribution statement

Shelby L. Ziegler: Formal analysis, Data curation, Writing – original draft, Writing – review & editing. **Rachel O. Brooks:** Investigation, Methodology, Writing – original draft, Writing – review & editing. **Scott L. Hamilton:** Data curation, Writing – original draft, Writing – review & editing. **Benjamin I. Ruttenberg:** Data curation, Writing – original draft, Writing – review & editing. **Jennifer A. Chiu:** Investigation, Methodology, Writing – original draft, Writing – review & editing. **Ryan T. Fields:** Investigation, Methodology, Writing – original draft, Writing – review & editing. **Grant T. Waltz:** Investigation, Methodology, Writing – original draft, Writing – review & editing. **Chenchen Shen:** Resources, Writing – original draft, Writing – review & editing. **Dean E. Wendt:** Conceptualization, Writing – original draft, Writing – review & editing. **Richard M. Starr:** Conceptualization, Writing – original draft, Writing – review & editing.

Declaration of competing interest

The authors declare no competing interests.

Acknowledgements

This research was made possible by the investment and dedication of the collaborating Commercial Passenger Fishing Vessel captains and crew, more than 100 people who served as science crew, and more than 1100 volunteer anglers. C. Barnes, K. Green, A. Greenley, C. Marks, K. Schmidt, and N. Yochum were especially important in the development of CCFRP. This work was supported by the California Ocean Protection Council and California Sea Grant [Grants no. C0752003 and R/MPA-45]. We would also like to thank the California Coastal and Marine Initiative of the Resources Legacy Fund Foundation, the California Department of Fish and Wildlife, the California Sea Grant College Program, the David and Lucile Packard Foundation, the Keith Campbell Foundation for the Environment, FishWise, and Santa Monica Seafood for historic funding to the CCFRP program. Additional project partners included the NOAA National Marine Fisheries Service, Coastal Conservation Association, California Department of Fish and Wildlife Marine Protected Areas Management Team and Natural Resource Volunteer Program, California State Parks, Central Coast Sportfishing, Coastside Fishing Club, Half Moon Bay Fisherman's Association, Morro Bay Commercial Fishermen's Association, National Marine Sanctuaries

Foundation, and The Nature Conservancy.

Appendix A. Supplementary figures

Supplementary figures to this article can be found online at https://doi.org/10.1016/j.biocon.2022.109546.

References

Addison, P.F.E., Flander, L.B., Cook, C.N., 2015. Are we missing the boat? Current uses of long-term biological monitoring data in the evaluation and management of marine protected areas. J. Environ. Manag. 149, 148–156. https://doi.org/10.1016/j.jenvman.2014.10.023.

Agardy, T., Di Sciara, G.N., Christie, P., 2011. Mind the gap: addressing the shortcomings of marine protected areas through large scale marine spatial planning. Mar. Policy 35, 226–232.

Alós, J., Puiggrós, A., Díaz-Gil, C., Palmer, M., Rosselló, R., Arlinghaus, R., 2015. Empirical evidence for species-specific export of fish Naïveté from a no-take marine protected area in a coastal recreational hook and line fishery. PLOS ONE 10, e0135348. https://doi.org/10.1371/journal.pone.0135348.

Babcock, R.C., Shears, N.T., Alcala, A.C., Barrett, N.S., Edgar, G.J., Lafferty, K.D., McClanahan, T.R., Russ, G.R., 2010. Decadal trends in marine reserves reveal differential rates of change in direct and indirect effects. PNAS 107, 18256–18261. https://doi.org/10.1073/pnas.0908012107.

Barceló, C., White, J.W., Botsford, L.W., Hastings, A., 2021. Projecting the timescale of initial increase in fishery yield after implementation of marine protected areas. ICES J. Mar. Sci. https://doi.org/10.1093/icesjms/fsaa233.

Bosch, N.E., Monk, J., Goetze, J., Wilson, S., Babcock, R.C., Barrett, N., Clough, J., Currey-Randall, L.M., Fairclough, D.V., Fisher, R., Gibbons, B.A., Harasti, D., Harvey, E.S., Heupel, M.R., Hicks, J.L., Holmes, T.H., Huveneers, C., Ierodiaconou, D., Jordan, A., Knott, N.A., Malcolm, H.A., McLean, D., Meekan, M., Newman, S.J., Radford, B., Rees, M.J., Saunders, B.J., Speed, C.W., Travers, M.J., Wakefield, C.B., Wernberg, T., Langlois, T.J., 2021. Effects of human footprint and biophysical factors on the body-size structure of fished marine species. Conserv. Biol. https://doi.org/10.1111/cobi.13807.

Brown, C.J., Mellin, C., Edgar, G.J., Campbell, M.D., Stuart-Smith, R.D., 2021. Direct and indirect effects of heatwaves on a coral reef fishery. Glob. Chang. Biol. 27, 1214–1225. https://doi.org/10.1111/gcb.15472.

California Ocean, Science Trust and California Department of Fish and Wildlife, 2013. State of the California Central Coast: Results from Baseline Monitoring of Marine Protected Areas 2007–2012. California, USA. https://caseagrant.ucsd.edu/sites/default/files/news/field_attachment/2015/cc_results_report.pdf.

Caselle, J.E., Rassweiler, A., Hamilton, S.L., Warner, R.R., 2015. Recovery trajectories of kelp forest animals are rapid yet spatially variable across a network of temperate marine protected areas. Sci. Rep. 5, 14102. https://doi.org/10.1038/srep14102.

Caselle, J.E., Wilson, J.R., Carr, M.H., Malone, D.P., Wendt, D.E., 2010. Can we predict interannual and regional variation in delivery of pelagic juveniles to nearshore popualtions of rockfishes (genus Sebates) using simple proxies of ocean conditions?. In: Reports of California Cooperative Oceanic Fisheries Investigations, 51, pp. 91–105.

Checkley, D.M., Barth, J.A., 2009. Patterns and processes in the California Current System. In: Progress in Oceanography, Eastern Boundary Upwelling Ecosystems: Integrative and Comparative Approaches, 83, pp. 49–64. https://doi.org/10.1016/j.pocean.2009.07.028.

da Silva, I.M., Hill, N., Shimadzu, H., Soares, A.M.V.M., Dornelas, M., 2015. Spillover effects of a community-managed marine reserve. PLOS ONE 10, e0111774. https://doi.org/10.1371/journal.pone.0111774.

Edgar, G.J., Stuart-Smith, R.D., Willis, T.J., Kininmonth, S., Baker, S.C., Banks, S., Barrett, N.S., Becerro, M.A., Bernard, A.T.F., Berkhout, J., Buxton, C.D., Campbell, S. J., Cooper, A.T., Davey, M., Edgar, S.C., Försterra, G., Galván, D.E., Irigoyen, A.J., Kushner, D.J., Moura, R., Parnell, P.E., Shears, N.T., Soler, G., Strain, E.M.A., Thomson, R.J., 2014. Global conservation outcomes depend on marine protected areas with five key features. Nature 506, 216–220. https://doi.org/10.1038/nature13022.

Freedman, R.M., Brown, J.A., Caldow, C., Caselle, J.E., 2020. Marine protected areas do not prevent marine heatwave-induced fish community structure changes in a temperate transition zone. Sci. Rep. 10, 21081. https://doi.org/10.1038/s41598-020-77885-3.

Gaines, S.D., White, C., Carr, M.H., Palumbi, S.R., 2010. Designing marine reserve networks for both conservation and fisheries management. PNAS 107, 18286–18293. https://doi.org/10.1073/pnas.0906473107.

Gill, D.A., Mascia, M.B., Ahmadia, G.N., Glew, L., Lester, S.E., Barnes, M., Craigie, I., Darling, E.S., Free, C.M., Geldmann, J., Holst, S., Jensen, O.P., White, A.T., Basurto, X., Coad, L., Gates, R.D., Guannel, G., Mumby, P.J., Thomas, H., Whitmee, S., Woodley, S., Fox, H.E., 2017. Capacity shortfalls hinder the performance of marine protected areas globally. Nature 543, 665–669. https://doi.org/10.1038/nature21708.

Goetze, J.S., Wilson, S., Radford, B., Fisher, R., Langlois, T.J., Monk, J., Knott, N.A., Malcolm, H., Currey-Randall, L.M., Ierodiaconou, D., Harasti, D., Barrett, N., Babcock, R.C., Bosch, N.E., Brock, D., Claudet, J., Clough, J., Fairclough, D.V., Heupel, M.R., Holmes, T.H., Huveneers, C., Jordan, A.R., McLean, D., Meekan, M., Miller, D., Newman, S.J., Rees, M.J., Roberts, K.E., Saunders, B.J., Speed, C.W., Travers, M.J., Treml, E., Whitmarsh, S.K., Wakefield, C.B., Harvey, E.S., 2021. Increased connectivity and depth improve the effectiveness of marine reserves. Glob. Chang. Biol. 27, 3432–3447. https://doi.org/10.1111/gcb.15635.

Graham, N.A.J., Robinson, J.P.W., Smith, S.E., Govinden, R., Gendron, G., Wilson, S.K., 2020. Changing role of coral reef marine reserves in a warming climate. Nat. Commun. 11, 2000. https://doi.org/10.1038/s41467-020-15863-z.

Guidetti, P., Baiata, P., Ballesteros, E., Franco, A.D., Hereu, B., Macpherson, E., Micheli, F., Pais, A., Panzalis, P., Rosenberg, A.A., Zabala, M., Sala, E., 2014. Large-scale assessment of Mediterranean marine protected areas effects on fish assemblages. PLOS ONE 9, e91841. https://doi.org/10.1371/journal.pone.0091841.

Hamilton, S.L., Caselle, J.E., Malone, D.P., Carr, M.H., 2010. Incorporating biogeography into evaluations of the Channel Islands marine reserve network. PNAS 107 (43), 18272–18277. https://doi.org/10.1073/pnas.0908091107.

Heupel, M.R., Simpfendorfer, C.A., 2005. Using acoustic monitoring to evaluate MPAs for shark nursery areas: the importance of long-term data. Mar. Technol. Soc. J. 39, 10–18. https://doi.org/10.4031/002533205787521749.

Ivens-Duran, M., 2014. A Spatial Analysis of Changes in Recreational Fishing Pressure on the Central Coast of California Subsequent to MPA Implementation. https://doi.org/10.15368/theses.2014.153. Master's Theses.

Jaco, E.M., Steele, M.A., 2020. Pre-closure fishing pressure predicts effects of marine protected areas. J. Appl. Ecol. 57, 229–240. https://doi.org/10.1111/1365-2664.13541.

Jarvis, E.T., Lowe, C.G., 2008. The effects of barotrauma on the catch-and-release survival of southern California nearshore and shelf rockfish (Scorpaenidae, Sebastes spp.). Can. J. Fish. Aquat. Sci. 65, 1286–1296. https://doi.org/10.1139/F08-071.

Jennings, S., 2000. Patterns and prediction of population recovery in marine reserves. Rev. Fish Biol. Fish. 10, 209–231. https://doi.org/10.1023/A:1016619102955.

Kellner, J.B., Tetreault, I., Gaines, S.D., Nisbet, R.M., 2007. Fishing the line near marine reserves in single and multispecies fisheries. Ecol. Appl. 17, 1039–1054. https://doi.org/10.1890/05-1845.

Knott, N.A., Williams, J., Harasti, D., Malcolm, H.A., Coleman, M.A., Kelaher, B.P., Rees, M.J., Schultz, A., Jordan, A., 2021. A coherent, representative, and bioregional marine reserve network shows consistent change in rocky reef fish assemblages. Ecosphere 12, e03447. https://doi.org/10.1002/ecs2.3447.

Lenihan, H.S., Gallagher, J.P., Peters, J.R., Stier, A.C., Hofmeister, J.K.K., Reed, D.C., 2021. Evidence that spillover from marine protected areas benefits the spiny lobster (Panulirus interruptus) fishery in southern California. Sci. Rep. 11, 2663. https://doi.org/10.1038/s41598-021-82371-5.

Lester, S.E., Halpern, B.S., Grorud-Colvert, K., Lubchenco, J., Ruttenberg, B.I., Gaines, S. D., Airamé, S., Warner, R.R., 2009. Biological effects within no-take marine reserves: a global synthesis. Mar. Ecol. Prog. Ser. 384, 33–46. https://doi.org/10.3354/meps08029.

Lotze, H.K., Guest, H., O'Leary, J., Tuda, A., Wallace, D., 2018. Public perceptions of marine threats and protection from around the world. Ocean Coast. Manag. 152, 14–22. https://doi.org/10.1016/j.ocecoaman.2017.11.004.

Lotze, H.K., Lenihan, H.S., Bourque, B.J., Bradbury, R.H., Cooke, R.G., Kay, M.C., Kidwell, S.M., Kirby, M.X., Peterson, C.H., Jackson, J.B.C., 2006. Depletion, degradation, and recovery potential of estuaries and coastal seas. Science 312, 1806–1809. https://doi.org/10.1126/science.1128035.

Love, M.S., Morris, P., McCrae, M., Collins, R., 1990. Life History Aspects of 19 Rockfish Species (Scorpaenidae: Sebastes) From the Southern California Bight. NOAA Technical Report NMFS 87.

Lynch, T.P., 2006. Incorporation of recreational fishing effort into design of marine protected areas. Conserv. Biol. 20, 1466–1476. https://doi.org/10.1111/j.1523-1739.2006.00509.x.

Lynch, T.P., 2014. A decadal time-series of recreational fishing effort collected during and after implementation of a multiple use marine park shows high inter-annual but low spatial variability. Fish. Res. 151, 85–90. https://doi.org/10.1016/j.fishres.2013.09.014.

Micheli, F., Saenz-Arroyo, A., Greenley, A., Vazquez, L., Montes, J.A.E., Rossetto, M., Leo, G.A.D., 2012. Evidence that marine reserves enhance resilience to climatic impacts. PLOS ONE 7, e40832. https://doi.org/10.1371/journal.pone.0040832.

Moffitt, E.A., White, J.W., Botsford, L.W., 2013. Accurate assessment of marine protected area success depends on metric and spatiotemporal scale of monitoring. Mar. Ecol. Prog. Ser. 489, 17–28. https://doi.org/10.3354/meps10425.

Murawski, S.A., Wigley, S.E., Fogarty, M.J., Rago, P.J., Mountain, D.G., 2005. Effort distribution and catch patterns adjacent to temperate MPAs. ICES J. Mar. Sci. 62, 1150–1167. https://doi.org/10.1016/j.icesjms.2005.04.005.

Nickols, K.J., White, J.W., Malone, D., Carr, M.H., Starr, R.M., Baskett, M.L., Hastings, A., Botsford, L.W., 2019. Setting ecological expectations for adaptive management of marine protected areas. J. Appl. Ecol. 56, 2376–2385. https://doi.org/10.1111/1365-2664.13463.

Nillos Kleiven, P.J., Espeland, S.H., Olsen, E.M., Abesamis, R.A., Moland, E., Kleiven, A. R., 2019. Fishing pressure impacts the abundance gradient of European lobsters across the borders of a newly established marine protected area. Proc. R. Soc. B Biol. Sci. 286, 20182455. https://doi.org/10.1098/rspb.2018.2455.

Ohayon, S., Granot, I., Belmaker, J., 2021. A meta-analysis reveals edge effects within marine protected areas. Nat. Ecol. Evol. https://doi.org/10.1038/s41559-021-01502-3.

Ojeda-Martinez, C., Bayle-Sempere, J.T., Sánchez-Jerez, P., Forcada, A., Valle, C., 2007. Detecting conservation benefits in spatially protected fish populations with meta-analysis of long-term monitoring data. Mar. Biol. 151, 1153–1161. https://doi.org/10.1007/s00227-006-0557-0.

Pollnac, R., Christie, P., Cinner, J.E., Dalton, T., Daw, T.M., Forrester, G.E., Graham, N.A. J., McClanahan, T.R., 2010. Marine reserves as linked social–ecological systems. PNAS 107, 18262–18265. https://doi.org/10.1073/pnas.0908266107.

Pressey, R.L., 1994. Ad hoc reservations: forward or backward steps in developing representative reserve systems? Conserv. Biol. 8, 662–668. https://doi.org/10.1046/j.1523-1739.1994.08030662.x.

R Core Team, 2021. R: a language and environment for statistical computing. URL. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Rassweiler, A., Costello, C., Siegel, D.A., 2012. Marine protected areas and the value of spatially optimized fishery management. PNAS 109, 11884–11889. https://doi.org/10.1073/pnas.1116193109.

Reed, D., Washburn, L., Rassweiler, A., Miller, R., Bell, T., Harrer, S., 2016. Extreme warming challenges sentinel status of kelp forests as indicators of climate change. Nat. Commun. 7, 13757. https://doi.org/10.1038/ncomms13757.

Saarman, E.T., Carr, M.H., 2013. The California marine life protection act: a balance of top down and bottom up governance in MPA planning. In: Marine Policy, Governing Marine Protected Areas: Towards Social-ecological Resilience Through Institutional Diversity, 41, pp. 41–49. https://doi.org/10.1016/j.marpol.2013.01.004.

Smale, D.A., Wernberg, T., Oliver, E.C.J., Thomsen, M., Harvey, B.P., Straub, S.C., Burrows, M.T., Alexander, L.V., Benthuysen, J.A., Donat, M.G., Feng, M., Hobday, A. J., Holbrook, N.J., Perkins-Kirkpatrick, S.E., Scannell, H.A., Sen Gupta, A., Payne, B. L., Moore, P.J., 2019. Marine heatwaves threaten global biodiversity and the provision of ecosystem services. Nat. Clim. Chang. 9, 306–312. https://doi.org/10.1038/s41558-019-0412-1.

Starr, R.M., Wendt, D.E., Barnes, C.L., Marks, C.I., Malone, D., Waltz, G., Schmidt, K.T., Chiu, J., Launer, A.L., Hall, N.C., Yochum, N., 2015. Variation in responses of fishes across multiple reserves within a network of marine protected areas in temperate waters. PLOS ONE 10, e0118502. https://doi.org/10.1371/journal.pone.0118502.

Starr, R.M., Wendt, D.E., Mulligan, T., Tyburczy, J., Morgan, S., Hamilton, S.L., Ruttenberg, B.I., Caselle, J.E., Semmens, B.X., Bellquist, L., 2021. Nearshore Fishes Abundance and Distribution Data, California Collaborative Fisheries Research Program (CCFRP), 2007-2020. California Ocean Protection Council Data Repository. https://doi.org/10.25494/P6901R.

Thamp, V.A., Anand, M., Bauch, C.T., 2018. Socio-ecological dynamics of Caribbean coral reef ecosystems and conservation opinion propagation. Sci. Rep. 8 (1), 2597. https://doi.org/10.1038/s41598-018-20341-0.

Wendt, D.E., Starr, R.M., 2009. Collaborative research: an effective way to collect data for stock assessments and evaluate marine protected areas in California. Mar. Coast. Fish. 1, 315–324. https://doi.org/10.1577/C08-054.1.

White, J.W., Botsford, L.W., Baskett, M.L., Barnett, L.A., Barr, R.J., Hastings, A., 2011. Linking models with monitoring data for assessing performance of no-take marine reserves. Front. Ecol. Environ. 9, 390–399. https://doi.org/10.1890/100138.

White, J.W., Botsford, L.W., Moffitt, E.A., Fischer, D.T., 2010. Decision analysis for designing marine protected areas for multiple species with uncertain fishery status. Ecol. Appl. 20, 1523–1541. https://doi.org/10.1890/09-0962.1.

Wood, S.N., 2011. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. J. R. Stat. Soc. Ser. B 73, 3–36.

Worm, B., Barbier, E.B., Beaumont, N., Duffy, J.E., Folke, C., Halpern, B.S., Jackson, J.B. C., Lotze, H.K., Micheli, F., Palumbi, S.R., Sala, E., Selkoe, K.A., Stachowicz, J.J., Watson, R., 2006. Impacts of biodiversity loss on ocean ecosystem services. Science 314, 787–790. https://doi.org/10.1126/science.1132294.

Worm, B., Hilborn, R., Baum, J.K., Branch, T.A., Collie, J.S., Costello, C., Fogarty, M.J., Fulton, E.A., Hutchings, J.A., Jennings, S., Jensen, O.P., Lotze, H.K., Mace, P.M., McClanahan, T.R., Minto, C., Palumbi, S.R., Parma, A.M., Ricard, D., Rosenberg, A. A., Watson, R., Zeller, D., 2009. Rebuilding global fisheries. Science 325, 578–585. https://doi.org/10.1126/science.1173146.

Yochum, N., Starr, R.M., Wendt, D.E., 2011. Utilizing fishermen knowledge and expertise: keys to success for collaborative fisheries research. Fisheries 36, 593–605. https://doi.org/10.1080/03632415.2011.633467.

Glossary (definitions of field specific terms)

BPUE: biomass per unit effort measured as the total weight of fish in kilograms captured per number of hours fished by anglers (kg angler h^{-1}).

Fishing naivete: fish located in areas closed to fishing (i.e., reserves) are unfamiliar with fishing gear and therefore may be more vulnerable to exploitation.

Marine protected area (MPA): a broad term for a marine or estuarine area where removing natural or cultural resources is limited or prohibited.