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Evaluating the influence of marine protected areas on surf zone fish

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Abstract

Marine protected areas (MPAs) globally serve conservation and fisheries management goals, generating positive effects in some marine ecosystems. Surf zones and sandy beaches, critical ecotones bridging land and sea, play a pivotal role in the life cycles of numerous fish species and serve as prime areas for subsistence and recreational fishing. Despite their significance, these areas remain understudied when evaluating the effects of MPAs. We compared surf zone fish assemblages inside and outside MPAs across 3 bioregions in California (USA). Using seines and baited remote underwater videos (BRUVs), we found differences in surf zone fish inside and outside MPAs in one region. Inside south region MPAs, we observed higher abundance (Tukey's honest significant difference [HSD] = 0.83, $p = 0.0001$) and richness (HSD = 0.22, $p = 0.0001$) in BRUVs and greater biomass (HSD = 0.32, $p = 0.0002$) in seine surveys compared with reference sites. Selected live-bearing, fished taxa were positively affected by MPAs. Elasmobranchs displayed greater abundance in BRUV surveys and higher biomass in seine surveys inside south region MPAs (HSD = 0.35, $p = 0.0003$ and HSD = 0.23, $p = 0.008$, respectively). Although we observed no overall MPA signal for Embiotocidae, abundances of juvenile and large adult barred surfperch (*Amphistichus argenteus*), the most abundant fished species, were higher inside MPAs (K–S test $D = 0.19$, $p < 0.0001$). Influence of habitat characteristics on MPA performance indicated surf zone width was positively associated with fish abundance and biomass but negatively associated with richness. The south region had the largest positive effect size on all MPA performance metrics. Our findings underscored the variability in species richness and composition across regions and survey methods that significantly affected differences observed inside and outside MPAs. A comprehensive assessment of MPA performance should consider specific taxa, their distribution, and the effects of habitat factors and geography.

KEYWORDS

beach seines, BRUVs, community composition, marine protected areas, surf zone fish

INTRODUCTION

Marine protected areas (MPAs) have been widely implemented over the past few decades to conserve and restore fisheries and marine ecosystems (Gaines et al., 2010; Halpern et al., 2019; Lubchenco & Grorud-Colvert, 2015; Ruckelshaus et al., 2008). Studies of the effectiveness of MPAs in achieving conservation goals show a range of results, including increased biomass, abundance, average body size, and diversity of marine species inside reserves (Claudet et al., 2008; Ferreira et al., 2022;

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Kirkman et al., 2021; Lester et al., 2009; Micheli et al., 2004; Sale et al., 2005). Despite these promising results, the direction and magnitude of measured MPA effects depend on MPA parameters (Caselle et al., 2015; Côté et al., 2001), including reserve size (Claudet et al., 2008; Halpern, 2003; Parnell et al., 2006), spacing (Halpern & Warner, 2003; Shanks et al., 2003), shape (Kramer & Chapman, 1999), and age (Edgar et al., 2014; Molloy et al., 2009). Social factors, including level of enforcement (Gill et al., 2017; Guidetti et al., 2008; Turnbull et al., 2018), stakeholder support (Di Franco et al., 2016; Walmsley & White, 2003), and intensity of fishing pressure in surrounding areas (Ziegler et al., 2022), can also influence the effectiveness of MPAs. Ecological benefits of MPAs may be apparent quickly or require decades to manifest (Grorud-Colvert et al., 2021; Hopf & White, 2023; White et al., 2013). Furthermore, individual taxa and trophic groups may respond to MPA protection at different rates depending on population status, past and present fishing pressure, and life-history traits, including reproductive mode, dispersal, and recruitment patterns (Fernández-Chacón et al., 2021; Micheli et al., 2004). The complexity of factors influencing the effectiveness of MPAs can make measuring and interpreting MPA success difficult, yet understanding how different factors influence the ecological effectiveness of MPAs is crucial for adaptive management decisions.

Using scientific recommendations and stakeholder input, the state of California designed and implemented an extensive network of MPAs that covers over 16% of state waters (CDFW, 2022; OPC, 2022; Saarman & Carr, 2013). To assess the effectiveness of these protected areas for enhancing abundance, biomass, and diversity of species targeted by fisheries, baseline studies and monitoring were conducted across multiple habitat types (e.g., kelp forests, rocky-reefs, Caselle et al., 2015; Starr et al., 2015). Although sandy beaches and surf zones were not initially prioritized in MPA design, they constitute a critical and readily accessible fishery, and the majority of California coastal MPAs include these habitats as a significant portion of the shoreline. However, the majority of sandy beaches and surf zones in California's MPAs have not been comprehensively surveyed to evaluate MPA success. With limited baseline surveys of fish assemblages in surf zones prior to MPA implementation (Nielsen et al., 2013, 2017), assessing MPAs for this ecosystem is an important yet challenging objective.

Sandy beaches and surf zones are a widespread coastal ecosystem, making up 31% of ice-free shorelines worldwide (Luijendijk et al., 2018) and up to 93% of shorelines in southern California (Dugan et al., 2000). These edge ecosystems connecting land and sea are lost to urbanization, development, and climate-change-induced sea-level rise (Schlacher et al., 2007; Vitousek et al., 2017; Vousdoukas et al., 2020), endangering beach biodiversity (Defeo et al., 2009; Schooler et al., 2019). Surf zones, the shallow areas where waves break before reaching shore, harbor diverse biotic communities that include ecologically, culturally, and economically important fish species (Olds et al., 2018) that attract recreational anglers and support significant artisanal and subsistence fisheries worldwide (Defeo, 2003; Schlacher et al., 2015). Surf zones are critical habitat for a variety of fish species, serving as nursery (Lombardi et al., 2014; Nanami & Endo, 2007), foraging (Tatematsu et al., 2014), and spawning habitats, often hosting unique species adapted for these high-energy environments (Hirose & Kawaguchi, 1998; Krueger et al., 2010; McLachlan & Brown, 2006).

Although these dynamic coastal interfaces are broadly recognized for their ecosystem services, their intrinsic importance and function are often less apparent in coastal monitoring, management, and conservation planning (Dugan et al., 2010; Harris et al., 2014), leaving gaps in understanding of their current status, trends, and future trajectories (Dugan et al., 2010; Fanini et al., 2020; Nel et al., 2014). For example, fish assemblages in surf zones are far less studied than their counterparts in neighboring ecosystems, such as rocky reefs (Banks & Skilleter, 2007; Harris et al., 2015; McLachlan & Brown, 2006), and data on surf zone fish assemblages are rare, incomplete, or nonexistent in many regions, including California (Allen & Pondella, 2006; Carlisle et al., 1960; Crawley et al., 2006; Marin Jarrin & Miller, 2013; Olds et al., 2018). Although studies are limited, evaluations of the effects of MPAs on surf zone fishes report significantly higher densities, greater biomass, and larger body sizes of fish in no-take reserves than in areas open to fishing (Attwood et al., 2016; Bullock et al., 2021; Venter & Mann, 2012 [South Africa]; Ortodossi et al., 2019 [Australia]). Several factors inherent to surf zones can complicate the interpretation of results (Mann et al., 2016). Surf zone fish assemblages often exhibit high temporal variation with changes in season, diel period, and tidal state (Beyst et al., 2002; Koval, 2022; Layman, 2000), as well as spatial variation in response to environmental factors, microhabitat characteristics of the beach (Crawley et al., 2006; McLachlan & Brown, 2006), and proximity to adjacent ecosystems (Henderson et al., 2022; Mosman et al., 2020; Ortodossi et al., 2019). High variability in abundance and species composition is often considered a defining characteristic of surf zone fish assemblages (Clark et al., 1996; Ross et al., 1987), and it creates challenges for detecting MPA effects.

Life-history traits, including reproductive mode, dispersal, recruitment patterns, species interactions, and fishing pressure, are predicted to influence the strength of MPA effects (Fernández-Chacón et al., 2021; Fisher & Frank, 2002; Micheli et al., 2004). In California, many species of nearshore elasmobranchs are currently or were historically targeted by both recreational and commercial anglers (Allen et al., 2002; Hill & Schneider, 1999; Jarvis et al., 2004), including leopard sharks (*Triakis semifasciata*), which exhibit site fidelity and use coastal MPAs (Carlisle & Starr, 2009; Launer, 2014; Norse, 2010; Nosal et al., 2013). The low fecundity and largely local reproduction of elasmobranchs (Camhi, 1998), including the smaller species observed in surf zones, plus their vulnerability to overfishing and stock collapse (Stevens et al., 2000) have led to broadly recognized conservation concerns for this targeted group (Jorgensen et al., 2022; MacNeil et al., 2020; Musick et al., 2000). The same characteristics that make them vulnerable to overfishing also make them good candidates for measuring ecological signals of MPAs (Bond et al., 2012; McCook et al., 2010; Speed et al., 2018). Similarly, surfperches (Embiotocidae) are targeted by anglers in the surf zone, and they are characterized by life-history traits that make them more vulnerable to

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overexploitation. These traits include a viviparous reproductive mode, whereby surfperch produce small numbers of relatively large, well-developed juveniles (Baltz, 1984; Carlisle et al., 1960; Love, 2011). In contrast to species with planktonic larval or juvenile stages that use a variety of marine habitats before maturing, newly born surfperch of several fished species remain in the adult habitat (surf zone) (Behrens, 1977; Bernardi, 2000). Adults of several surfperch species migrate to the shallow surf zones of sandy beaches to give birth (Carlisle et al., 1960). These life-history traits and a focal recreational shore fishery make surfperch potentially vulnerable to local fishing pressure and excellent candidates for evaluating effects of MPAs (Ortodossi et al., 2019).

Because sandy surf zones face increasing threats to habitat and biodiversity (Barnard et al., 2021; Vitousek et al., 2017), it is essential to understand the influence of spatial management approaches on these critical ecosystems. We aimed to evaluate the influence of California MPAs on surf zone fish assemblages following a decade of protection. We hypothesized that surf zone fish abundance, size structure, biomass, species richness, and species composition differ inside and outside MPAs and that biogeography, habitat availability, and MPA size modify the strength of these differences. We also predicted that fish taxa with limited life-stage dispersal (i.e., live bearing or egg laying groups), which are targeted by recreational shore fisheries, surfperch (Embiotocidae), and sharks and rays (Elasmobranchii), will exhibit greater abundance and biomass and different size distributions inside MPAs. We compared community metrics of composition, richness, abundance, and biomass of surf zone fish inside and outside MPAs with 2 complementary survey techniques (seines and baited remote underwater video [BRUV]) at sites spanning 1300 km of coastline across 3 bioregions in California. We then examined the factors contributing to MPA performance of each community metric inside MPAs. We predicted that surf zone habitat and MPA size would positively influence MPA performance.

METHODS

Survey sites

We surveyed surf zone fish assemblages inside and outside MPAs in a paired sampling design at 13 mainland coastal MPAs and paired reference sites across 3 bioregions (hereafter regions) (Figure 1). We defined MPAs as locations where harvesting of all surf zone fish is prohibited. However, 2 of our MPA sites, Reading Rock and Samoa, allow exemptions for subsistence fishing by local Indigenous people (CDFW, 2022) (Appendices S1 & S2). For each MPA study site, we selected a reference site that closely matched the geomorphology, orientation, and exposure of prevailing swell, length, habitat characteristics, and beach type of the MPA site (Dugan et al., 2022) located in the same littoral cell where possible (Patsch & Griggs, 2006) (Appendix S3). As a result, we established 13 MPA–reference site pairs (26 study sites in total) (Figure 1a–e; Table 1). Our 13 site pairs were distributed across 3 regions in California's MPA network—4 site pairs in the north, 4 in the central, and 5 in the south regions (Figure 1a–e). We used these regions as proxies for biogeographical and latitudinal patterns and because they were defined in part by management boundaries (Appendix S1).

Our study sites were all microtidal beaches of intermediate morphodynamic type that spanned a range of latitudes, landscapes, locations, exposures, beach lengths, and MPA characteristics (Dugan et al., 2022) (Appendices S1 & S2). To evaluate the correspondence of the MPA and reference site pairs in our paired design, we compared several environmental characteristics, including surf zone width, swash zone width, and swash period. We measured these variables during our surveys and sea surface temperature (SST) and productivity (chlorophyll a) from satellite imagery (Chin et al., 2017; Sathyendranath et al., 2019) (Appendix S3). These key habitat characteristics differed across MPAs but were similar between each MPA and their paired reference site (Appendix S3), and all values were within range of our expectations for intermediate morphodynamic-type beaches (Nielsen et al., 2017; Short, 1996). For example, Whaler's Cove (MPA) and Stillwater Cove (reference) had median surf zone widths of 13.3 and 11.5 m, median SST of 15.25 and 15.36°C, and median daily chlorophyll a of 1.95 and 1.97 (Appendix S3), respectively, and were similar in length of sandy beach (0.41 and 0.44 km, respectively) (Appendix S1). These comparisons showed the high congruence of our paired MPA and reference sites and the effectiveness of our paired sampling design in reducing the physical and environmental differences in each site pair.

Field methods

We conducted surveys of surf zone fish at each site 3 times from summer to fall in 2019 and 2020 (2–4 weeks between surveys) (Appendix S1). Due to ocean conditions, some surveys in the south occurred later in the fall than other regions in 2019. Survey in the north started 2–3 weeks before those in the central and south regions in 2020 (Appendix S1). Despite this slight offset in timing of surveys, we did not observe large differences in environmental conditions within a region across survey dates but did observe differences in SST across regions (Appendix S4). Recorded temperatures ranged from 11.28 to 16.33°C, 12.86 to 17.04°C, and 14.79 to 24.99°C in the north, central, and south regions, respectively (Appendix S4). Surf zone fish assemblages in the central region are similar across these 2 seasons (G.K., personal observation). Surveys were conducted during standardized tide windows ($\leq$1 m) when the surf was relatively calm (i.e., small breaker waves). We used 2 complementary methods to quantify fish assemblages: beach seines and BRUV cameras (Figure 1f,g). Our beach seines had a maximum effective sampling depth of <1–1.5 m, and the BRUVs had a minimum effective depth of 2–3 m in the surf zone. This sampling design allowed us to survey different segments of the surf zone fish community. The BRUVs surveyed fishes at approximately twice the water depth of seines.

Six seines (nets were 15.25 × 1.8 m with 1-cm mesh, poles were attached on each end, the central bag was

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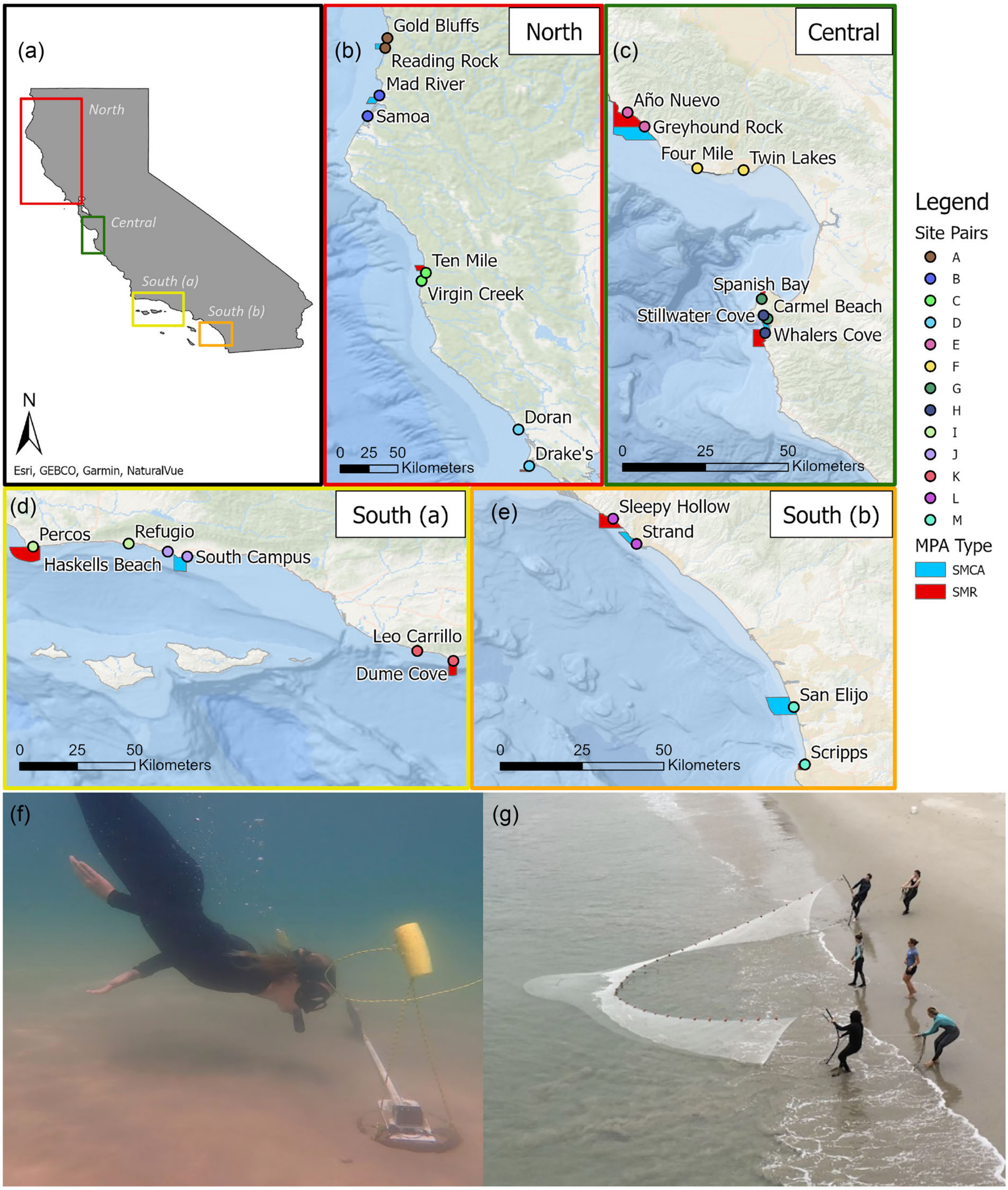

FIGURE 1 Study site locations (a) along the California (USA) coast and in (b) north, (c) central, and (d, e) south regions (site pairs are the same color; MPA, marine protected area; SMCA, state marine conservation area; SMR, state marine reserve); (f) diver deploying a BRUV on sandy benthos in deep surf zone (photo by Walter Heady); and (g) researchers bringing in a seine tow in shallow surf zone (photo by Jenifer Dugan).

1.8 × 1.8 × 1.8 m) were towed along the beach at each site on every survey date (Figure 1f). Fish from each tow were identified, counted, and measured (standard length, total length [TL], or both for the first 30 individuals of each species per tow) before being released at the capture site. Our research design was approved by the University of California Santa Barbara (943), California State Polytechnic University, Humbolt (2020F66-A), and San Jose State University (1065). Biomass estimation for each species was performed using the length measurements and published species-specific length–weight relationships (Froese & Pauly, 2022). If no empirical relationship was available, model fit relationships based on species of

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similar body morphology were used (Froese & Pauly, 2022; Pauly & Froese, 2006). Fish that could not be identified were not included in biomass measurements.

The BRUVs consisted of a single GoPro video camera (GoPro Inc.) mounted on a 4.5-kg flat weight attached to a 1-m PVC pole with a bait bag containing 150 g of chopped squid within the camera's field of view (Harvey et al., 2007, 2013; Koval, 2022) (Figure 1g; Shah Esmaeili et al., 2021; Vargas-Fronseca et al., 2016). Six regularly spaced (at least 15 m, but typically >50 m apart, depending on amount of sandy subtidal area available at each site) BRUVs were deployed on sand along a transect parallel to shore (Gold et al., 2023; Honeyman et al., 2023; Shah Esmaeili et al., 2021) (Appendices S5 & S6). At some sites, the high-energy environment of the shallow surf zone reduced the accuracy of BRUV videos; therefore, we placed BRUVs in deeper water near the outer edge of these surf zones (Appendix S5). Each BRUV recorded video for at least 70 min, resulting in a sample duration of 1 h per BRUV (after a 10-min acclimation period).

Fish abundance was quantified from BRUV video footage with a standard MaxN (maximum number) statistic (Murphy & Jenkins, 2010; Whitmarsh et al., 2017), which represents the maximum number of individuals of the same species observed in a single video frame. The MaxN is a conservative metric that avoids double counting individuals that may reappear at different times during an observation period. In cases where nearshore turbidity limited species identification, we reported the lowest known taxonomic unit. To prevent double counting of species due to these unidentified individuals, we calculated species richness as the number of unique taxa (similar to MaxN), excluding unknown individuals if a species of that group was also identified in the same video. The BRUV video data were processed using EventMeasure software (SeaGIS) for the central and south coast sites and manually for the north coast sites. Our calibration of these 2 approaches yielded consistent results.

Biological metrics

To evaluate biological characteristics of surf zone fish assemblages, our field survey observations were standardized to per unit effort metrics. Abundance was standardized as catch per unit effort (CPUE) in seine surveys and MaxN per unit effort (CPUE BRUV) in BRUV surveys. The total number of fish observed on a survey date at a site was divided by the number of samples (seines or BRUVS) used on that survey date. Species richness was standardized as richness per unit effort (RPUE) in seine surveys and richness per unit effort (RPUE BRUV) in BRUV surveys. The total number of fish species observed on a survey date at a site was divided by the number of samples (seines or BRUVS) used on that survey date. Biomass was standardized as biomass per unit effort (BPUE) in seine surveys. The total biomass observed on a survey date at a site was divided by the number of samples (seines or BRUVS) used on that survey date.

In general, we conducted 6 seine tows and deployed 6 BRUVs on each of our 6 survey dates at each site. However, field conditions, equipment failures, and analysis time constraints resulted in a lower number of samples at some sites on some survey dates (Dugan et al., 2022). Additionally, due to wildfires in the area, one site pair (Ten Mile and Virgin Creek) could only be sampled twice during 2020; therefore, this pair had 5 survey dates. Each survey date at a specific site acted as our sample unit, resulting in a total of 154 samples for each metric (26 sites × 5–6 survey dates).

Analyses

All analyses were conducted in R 4.0.2 (R Core Team, 2020), and raw data are publicly available (DataOne, 2022; Dugan et al., 2022).

To examine differences in community composition among survey sites ($n = 25$ for community analyses), we used a nonmetric multidimensional scaling (nMDS) analysis on a Bray–Curtis similarity matrix (Oksanen et al.,2023). Prior to analysis, fish abundance was scaled using the standard deviation (x/SD) of each species' abundance. Two dimensions were used to reduce stress below 0.2. We examined community composition for both survey methods to examine the effects of MPA, region, and survey method. A 3-way permutational analysis of variance (PERMANOVA) was used to partition sources of variation in surf zone fish assemblages and assess significance of survey method (2 levels), MPA protection (2 levels), and region (3 levels) (sequentially, function adonis2) (Anderson, 2001; McArdle & Anderson, 2001). We then assessed which species contributed to differences among the assemblage groupings for all pairwise combinations of predictors with SIMilarity PERcentages analyses (SIMPER, function simper()). To reduce the impact of unidentified species on our results, we combined redtail (*Amphistichus rhodoterus*), silver (*Hyperprosopon ellipticum*), and unknown surfperch into one category, surfperch spp. Unknown surfperches were only reported on the north coast BRUVs due to poor visibility. Seines from this region indicated that redtail (*A. rhodoterus*) and silver surfperch (*H. ellipticum*) were common, making them the species of the unidentified individuals. We excluded Virgin Creek seine surveys from our analyses where we observed only one fish. We repeated this entire procedure (nMDS, a sequential PERMANOVA, and SIMPER of all pairwise combinations of factors) to examine differences in community composition related to MPA status and region within each survey method independently because these methods showed very different community composition and abundance.

We investigated the influence of MPA status and region on ecological effectiveness of California MPAs for surf zone fish separately for each biological metric of richness, abundance, and BPEU. We used linear mixed-effect models with MPA status (2 levels) and region (3 levels) as fixed effects and site pair (13 levels) as a random effect ($n = 154$ for each analysis). Although our paired study design minimized environmental differences between MPA and reference within site pairs (Appendix S3),

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they encompassed much of the environmentally diverse coastline of California (Figure 1), resulting in inherent variability across site pairs. Our comparisons of select physical and environmental variables indicated large-scale geographic variability across regions, but rarely within site pairs (Appendices S3 & S4). For example, the north region was characterized by wider surf zones and lower SST than the south region, which typically showed narrower surf zones and higher SST (Appendix S4). In our system, region acted as a proxy not only for large-scale environmental variability, but also for shifts in fish species distributions (Horn & Allen, 1978; Miller, 2023; Spalding et al., 2007). For our design, site pair acted as a blocking factor to account for additional environmental variability not encompassed in the region term. Marginal R^2 is concerned with variance explained by fixed factors, whereas conditional R^2 is concerned with variance explained by the full model (both fixed and random factors) (Nakagawa & Schielzeth, 2013). By comparing marginal and conditional R^2 values, we inferred how much additional variability in our biological metrics the characteristics of a site pair might explain (Nakagawa & Schielzeth, 2013). Model formula for all mixed-effects models and additional analysis details are in Appendices. Multicollinearity between predictor variables, distributions of residuals, normality, and overdispersion were checked using variance inflation factors for mixed models, residual plots, and *Q*–*Q* plots and were all acceptable (Schielzeth et al., 2020). We report *F*-tests and pairwise post hoc comparisons based on Kenward–Roger approximation (Kenward & Roger, 2009).

We repeated these analyses to evaluate our hypotheses for 2 key groups of surf zone fish, elasmobranchs (in the south region only, 60 surveys) and surfperch (all regions, 154 surveys). We tested abundance metrics in both seines and BRUVs and biomass from seine surveys for each group. Analyses of elasmobranchs responses tested MPA status as a fixed effect because we only examined the south region. To explore possible patterns in fish body size inside and outside MPAs, we also compared size structure (TL) of 2 commonly encountered fish species, leopard sharks and barred surfperch (*Amphistichus argenteus*), observed in seine surveys (all regions aggregated) with a Kolmogorov–Smirnov test. Leopard sharks mature between 700 and 1200 mm (Ebert, 2003); therefore, we chose a middle measurement of 1100 mm as our separation of juvenile and adult life stages.

MPA performance

We examined the causal influence of width of surf zone (measured in situ on each survey date in meters), MPA size (length of protected shoreline in kilometers), and biogeography (region) on MPA performance. These predictor variables were chosen a priori based on previous surf zone fish and MPA performance studies in other regions (Edgar et al., 2014; Shah Esmaeili et al., 2022). To predict each MPA performance metric (per unit effort abundance, richness, biomass) for each survey method (BRUVs and seines), we used values of each of these predictor variables for our MPA sites ($n = 77$ for each metric). We used a structural causal modeling framework (Pearl, 2009) that employs directed acyclic graphs to visually represent causal structure of the study system (Arif & MacNeil, 2023; Laubach et al., 2021) (Figure 6a). We applied do-calculus principles and the backdoor criterion to guide covariate selection (Laubach et al., 2021; McElreath, 2020; Pearl, 2009). Our final linear models (one for each predictor variable of interest) and additional details are described in Appendices.

RESULTS

Community composition

The composition of surf zone fish assemblages varied significantly with survey method (PERMANOVA $F_{1,48} = 4.59$, $p = 0.0001$) (Figure 2a; Appendix S7). The BRUVs detected assemblage characteristic of deeper surf zones, including elasmobranch species, such as bat rays (*Myliobatis californica*), shovelnose guitarfish (*Pseudobatos productus*), flatfish (Pleuronectidae), and staghorn sculpin (*Leptocottus armatus*) (Figure 2a). In contrast, seines recorded assemblages typical of shallow surf zones, characterized by more species of surfperch, round stingray (*Urobatis halleri*), California corbina (*Menticirrhus undulatus*), and yellowfin croaker (*Umbrina roncador*) (Figure 2a). A subsequent SIMPER analyses highlighted specific species accounting for dissimilarities between survey methods (Appendix S8): barred surfperch, walleye surfperch (*Hyperprosopon argenteum*), and topsmelt (*Micrometrus minimus*) accounted for approximately 38% of the dissimilarity between BRUVs and seines. These species were relatively more common in seines (Appendix S8).

Both survey methods demonstrated significant variation in surf zone fish composition across regions (PERMANOVA $F_{(2,17)} = 2.84, p = 0.0001$ in seines and $F_{(2,20)} = 4.16, p = 0.0001$ in BRUVs; Figure 2c,e) but not as a function of MPA status (PERMANOVA $F_{(1,17)} = 0.77, p = 0.81$ in seines and $F_{(1,20)} = 0.75, p = 0.78$ in BRUVS; Figure 2d; Appendix S7). Barred surfperch was one of the top 5 most influential species in all comparisons tested in SIMPER analyses (Appendix S8). In seine surveys, barred surfperch and other Embiotocidae species differentiated north and central regions, Embiotocidae species and northern anchovy (*Engraulis mordax*) differentiated central and south regions, and Embiotocidae species and California corbina differentiated north and south regions. In seine surveys, barred surfperch was the most frequently occurring species, present at all but 4 sites (absent from Mad River, Samoa, and Ten Mile in the north and Whalers Cove in the central region). We observed barred surfperch in high numbers at multiple sites in the south and central regions in our seine surveys. For example, over the course of the study, we observed more than 1000 barred surfperch at Percos (MPA) in the south region. In BRUV surveys, barred and other surfperch also accounted for large portions of the separation between regions (Appendix S8).

Biological metrics

We observed 61 species of surf zone fish from 25 families in seine surveys and 67 species from 31 families in BRUV

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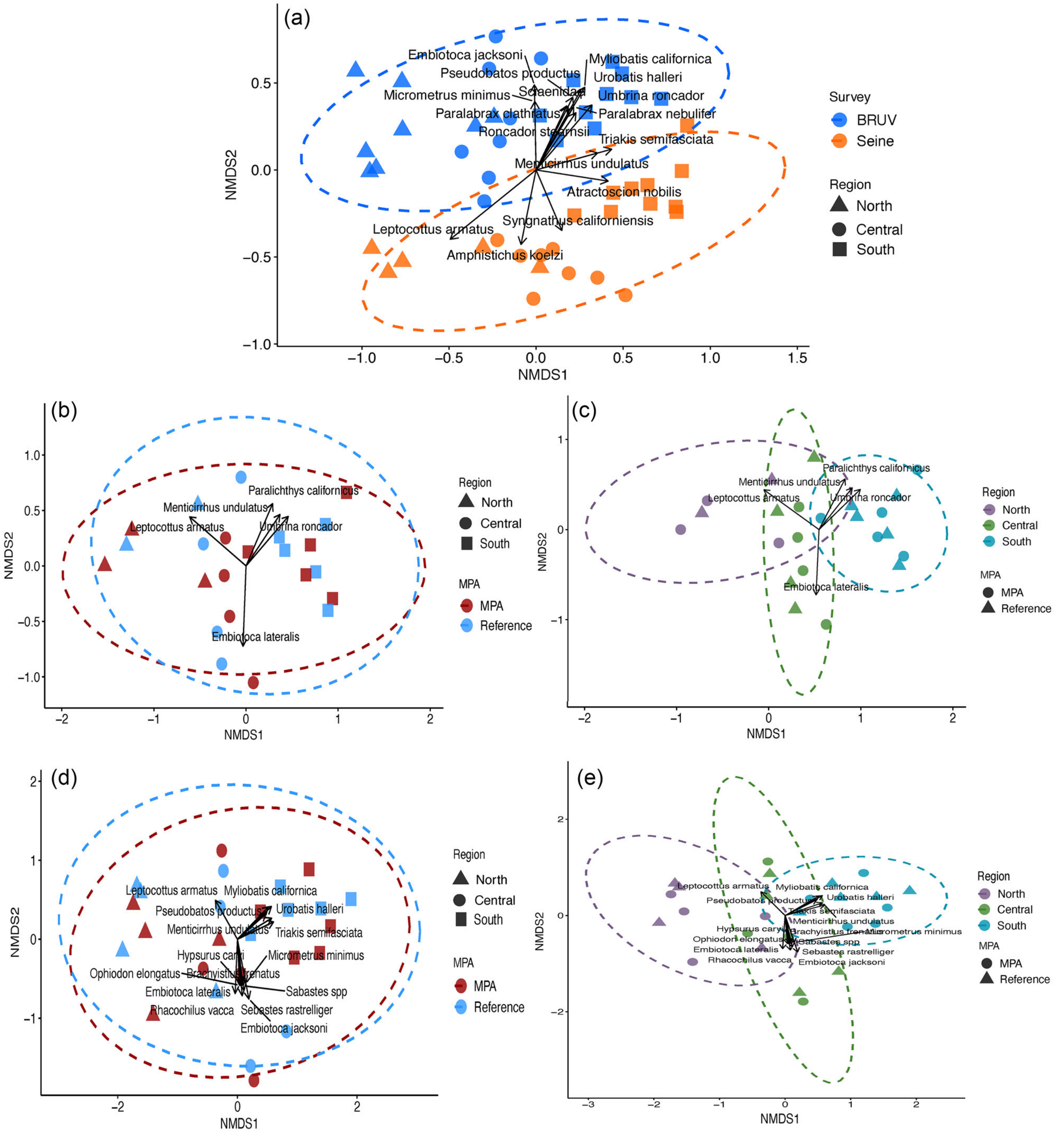

FIGURE 2 Community composition of surf zone fish at 25 study sites along the coast of California (USA): (a) comparison of results from seines and baited remote underwater video cameras (BRUVs). (b) Marine protected area (MPA) differences and (c) regional differences in community composition and relative abundance in seine surveys. (d) MPA differences and (e) regional differences in community composition and relative abundance in BRUV surveys. (Ellipses represent 95% confidence interval, species labeled, $p < 0.01$; arrows, significant vector loading of species [$p < 0.001$]; vector length, proportional to the correlation between ordination scores [nMDS 1, 2, or both] and the species in all panels).

surveys. We observed greater abundance, richness, and biomass of surf zone fish in MPAs than in reference sites in the south region (Figure 3). Differences in our biological metrics inside and outside MPAs varied with survey method (Appendix S9). We observed higher abundance (CPUE) in MPAs than in reference sites in the south region in BRUV surveys, but there was no consistent MPA signal in CPUE from seine surveys in any region (Figure 3g,h). A similar pattern was observed for richness; RPUE was higher in MPAs in the south region on BRUVs, but there were no differences in RPUE between MPA and reference sites in seine surveys in any region (Figure 3; Appendix S9). We observed high BPUE of surf zone fish

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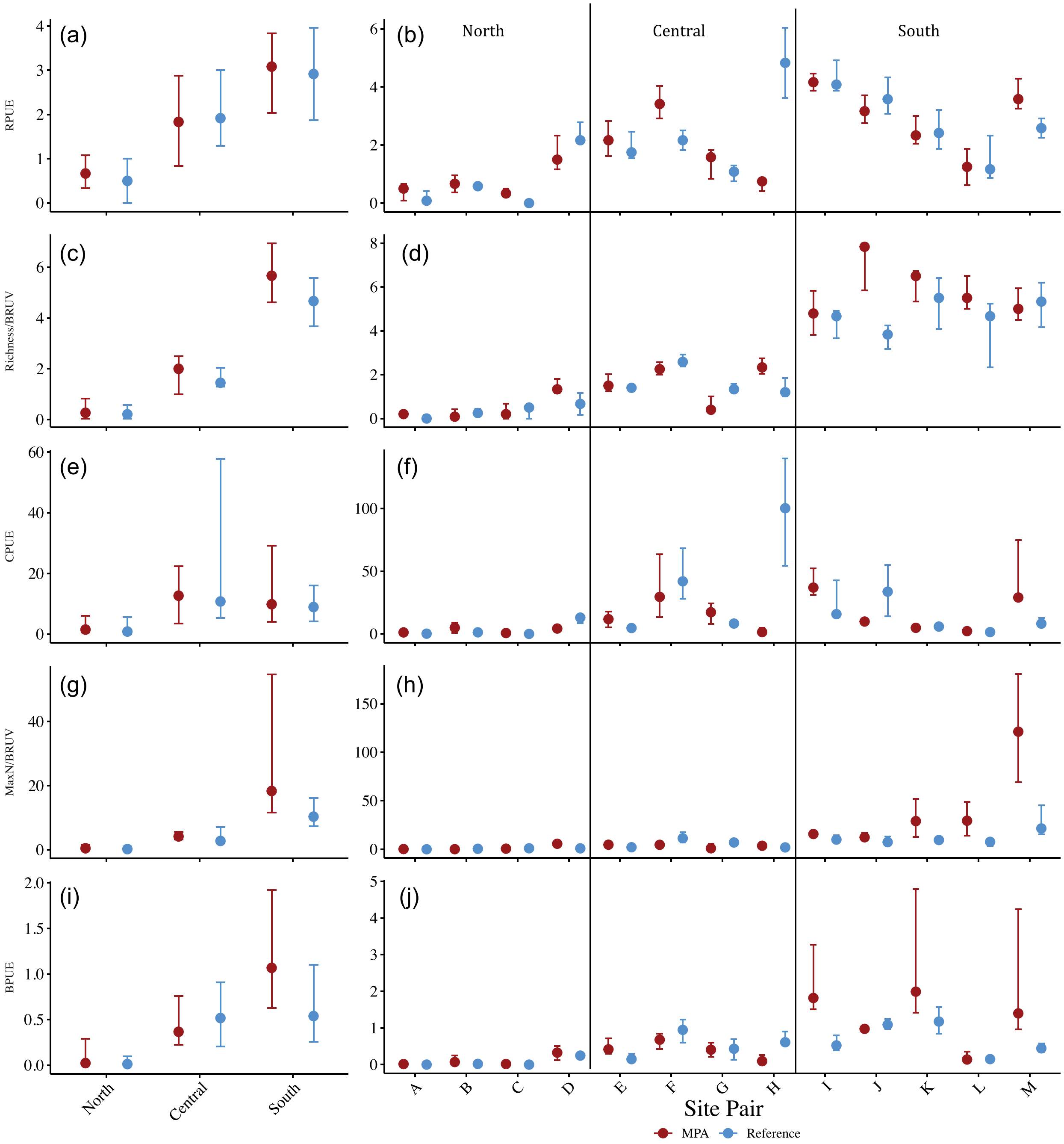

FIGURE 3 Median biological metrics of surf zone fish, (a) species richness per unit effort (RPUE) in seine sampling, (c) species richness per baited underwater video unit (richness/BRUV), (e) abundance as catch per unit effort (CPUE) in seines, (g) abundance as maximum number (MaxN) per unit effort with BRUV (MaxN/BRUV), and (i) biomass per unit effort (BPUE) in seine samples of all sampling events in each region in marine protected area (MPA) and reference sites (4 MPA and 4 reference sites in the north and central regions and 5 MPA and 5 reference sites in the south region). (b), (d), (f), (h), and (j), M biologiucaedian values of the same variables as in (a), (c), (e), (g), and (i) for all sampling events (6 events at all pairs except site pair [c], where there were 4) at each site in MPA and reference pairs (seine sampling: [a], [b], [e], [f], [i], [j]; BRUV sampling: [c], [d], [g], [h]; points, median; bars, first and third quartiles; site pairs ordered from north to south; see Appendix S1 for sites in each site pair).

measured in seines inside MPAs in the south region but not in the other 2 regions (Figure 3i).

We recorded a number of high-performing MPAs with differences in multiple metrics between MPA and reference sites for both survey methods in the south region (Figure 3). For example, BPUE was higher at Point Conception State Marine Reserve (SMR), Point Dume SMR, and Matlahuayl SMR than in their reference sites (Figure 3j). Similarly, we recorded higher CPUE BRUV at Point Dume SMR, Laguna Beach SMR, and Matlahuayl SMR compared with their reference sites (Figure 3h).

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TABLE 1 Marginal R^2 and conditional R^2 values for linear mixed-effects models of the effect of marine protected area (MPA) status and region on ecological effectiveness of California MPAs for surf zone fish.

Method	Metric	Marginal R^2	Conditional R^2
Seines	CPUE	0.23	0.51
	RPUE	0.35	0.65
	BPUE	0.33	0.52
	CPUE Elasmobranch	0.03	0.33
	BPUE Elasmobranch	0.09	0.3
	CPUE Embiotocidae	0.18	0.59
	BPUE Embiotocidae	0.10	0.42
BRUV	CPUE	0.61	0.73
	RPUE	0.77	0.83
	CPUE Elasmobranch	0.18	0.29
	CPUE Embiotocidae	0.12	0.46

Note: We investigated the effects of MPA status (MPA and reference) and region (north, central, south) on biological metrics with linear mixed-effects models with MPA status (2 levels) and region (3 levels) as fixed effects and site pair (13 levels) as a random effect. Marginal R^2 is concerned with variance explained by fixed factors, and conditional R^2 is concerned with variance explained by both fixed and random factors. Abbreviations: BPUE, biomass per unit effort; CPUE, catch per unit effort; RPUE, richness per unit effort.

Higher abundance in seine surveys was also observed at Matlahuayl SMR compared with its reference site, but this was not found for other pairs in the south region (Figure 3f). All metrics from both survey methods varied by region, with the north being significantly different from the south (Appendix S9). The south region exhibited the highest species richness compared with other regions in both seine and BRUV surveys (Figure 3a,c). The north region had the lowest richness, abundance, and biomass, and some sites in the central region had high values of richness, abundance, and biomass (Figure 3). However, no consistent MPA signal was detected in either region (Appendix S9).

Our mixed-effects model results highlighted the influence of site pairs on all biological metrics in seine surveys (Table 1). These models had conditional R^2 ranging from 0.51 to 0.65, with the portion attributed to fixed effects of MPA status and region (marginal R^2) ranging from 0.23 to 0.35 (Table 1). The addition of the random effect site pair strongly increased R^2 (conditional R^2) for abundance, richness, and biomass, emphasizing the influence of site pair location-specific characteristics on surf zone fish in seine surveys. In contrast, for BRUV surveys, the marginal R^2 was 0.61 for MaxN and 0.77 for richness compared with conditional R^2 of 0.73 and 0.83, respectively (Table 1). Our analysis of BRUV metrics demonstrated stronger influence of fixed effects, MPA, and region compared with seine surveys.

Elasmobranchs and surfperch

The majority of elasmobranchs we observed were in the south region; therefore, we focused our analyses on this region. We identified 5 species of Elasmobranchii in our seine surveys and an additional 3 species in our BRUV surveys (Appendix). Elasmobranchs, collectively, exhibited greater biomass and abundance in MPAs than in reference sites in the south region (Figure 4a,e,i; Appendix S10). Point Conception SMR, Campus Point SMCA, Point Dume SMR, and Matlahuayl SMR had greater abundances (CPUE in seines and MaxN in BRUVs) of elasmobranchs than their respective reference pairs (Figure 4b,f). The highest elasmobranch biomass recorded in our study was at Point Dume SMR; over 5 kg/seine were recorded on 2 survey dates (Figure 4j). Leopard sharks were the most abundant elasmobranch observed in seines (247 out of 278 fish), and all individuals were juveniles measuring 1 m or less in TL. The size distribution of leopard sharks observed in seines differed between MPAs and reference sites (K–S test $D = 0.63$, $p < 0.0001$); larger juvenile sharks (>350 mm) occurred more frequently in MPAs and smaller individuals (<350 mm) were more often in reference sites (Figure 5a). The largest individuals of this species were exclusively observed in MPAs (Figure 5a,c).

We observed 15 species of surfperch (Appendix) in seine surveys in all regions; peak collective abundance occurred in the central region (Figure 4c). The CPUE in seines and BRUV surveys did not vary between MPA and reference sites, and these metrics did not vary among regions (Figure 4c,g; Appendix S10). We also did not observe differences in surfperch BPUE among regions or between MPA and reference sites (Figure 4k). The highest BPUE of surfperch was observed at Point Conception (SMR) (Figure 4k). Barred surfperch was the most abundant targeted species of surf zone fish in our seine surveys; 2294 were caught in MPAs compared with 1840 in reference sites. Our seine surveys were nonselective for this species, resulting in the catch of more than twice as many juvenile fish (2856) compared with adult fish (1240). The overall size structure of barred surfperch differed between MPA and reference sites (K–S test $D = 0.19$, $p < 0.0001$); there was a higher proportion of large adults (TL > 300 mm) and juvenile fish (TL < 100 mm) in MPAs than in reference sites (Figure 5d).

MPA performance

The MPAs ranged from 0.66 to 58.34 km ^{2} and had shoreline lengths of 2.74 − 12.71 km (Appendices S1 & S2). In all surveys and metrics, MPA size had no or a negative association with our biological metrics; smaller MPAs (shorter protected shoreline) had higher values of the biological metrics (Figure 6). Surf zone width had small positive effects on CPUE (in both seines and BRUVs) and BPUE (Figure 6). There were more fish and higher fish biomass in MPAs with wide surf zones than in MPAs with narrow surf zones (Figure 6). In contrast, surf zone width exhibited negative effects on RPUE in both seine and BRUV surveys. We observed higher richness of fish at MPAs with narrow surf zones than in those with wide surf zones (Figure 6). Our results indicated a strong influence of region on MPA performance; the south region was the biggest predictor on all of our metrics across both seines and BRUVs (Figure 6).

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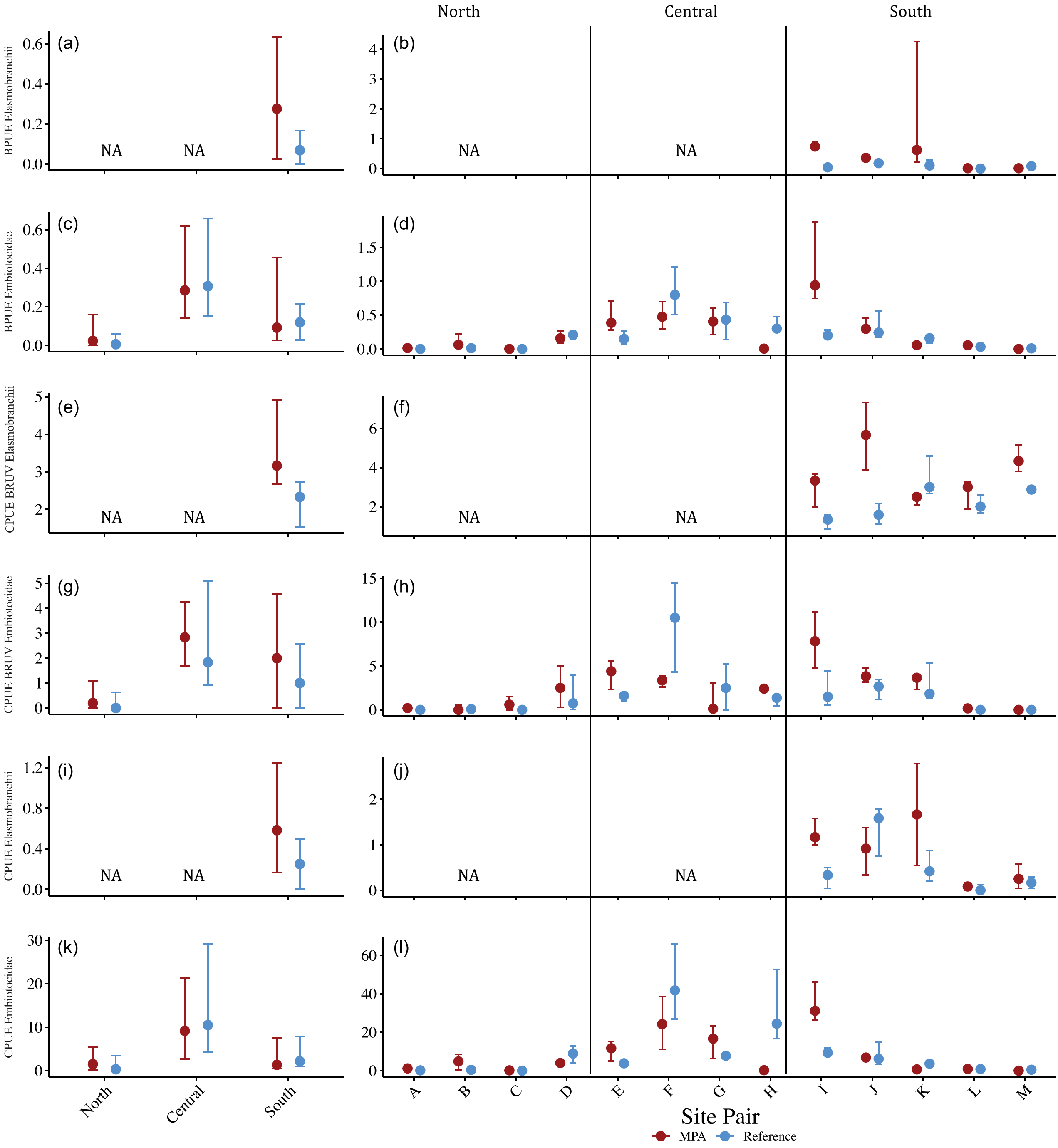

FIGURE 4 Median biolgical metrics of Elasmobrach and Surfperch in marine protected areas (MPAs) and reference sites: (a) Elasmobranchii biomass (biomass per unit effort [BPUE]) observed with seines, (c) Embiotocidae biomass (BPUE) observed with seines, (e) Elasmobranchii abundance (catch per unit effort [CPUE]) observed with baited underwater video (BRUVs), (g) Embiotocidae abundance (CPUE) observed with BRUVs, (i) Elasmobranchii abundance (CPUE) observed with seines, and (k) Embiotocidae abundance (CPUE) observed with seines. (b) (d) (f) (h) (j) and (l) Median valuesof all sampling events at each site in MPA and reference site pairs of the same variables as in (a), (c), (e), (g), (i) and (k) (6 events at all pairs except site pair [c], where there were 4) (seine sampling: [a], [b], [c], [d], [i], [j], [k], [l]; BRUV sampling: [e], [f], [g], [h]; points, median; bars, first and third quartiles; site pairs ordered from north to south; see Appendix S1 for sites in each site pair). For Embiotocidae surveys, *n* = 4 MPA and n = 4 reference sites in the north and central and *n* = 5 MPA and n = 5 reference sites in the south. Each site was surveyed on 5–6 dates resulting in 23 surveys in the north region, 24 surveys in the central region, and 30 surveys in the south region. Elasmobranchs were observed only in the south region.

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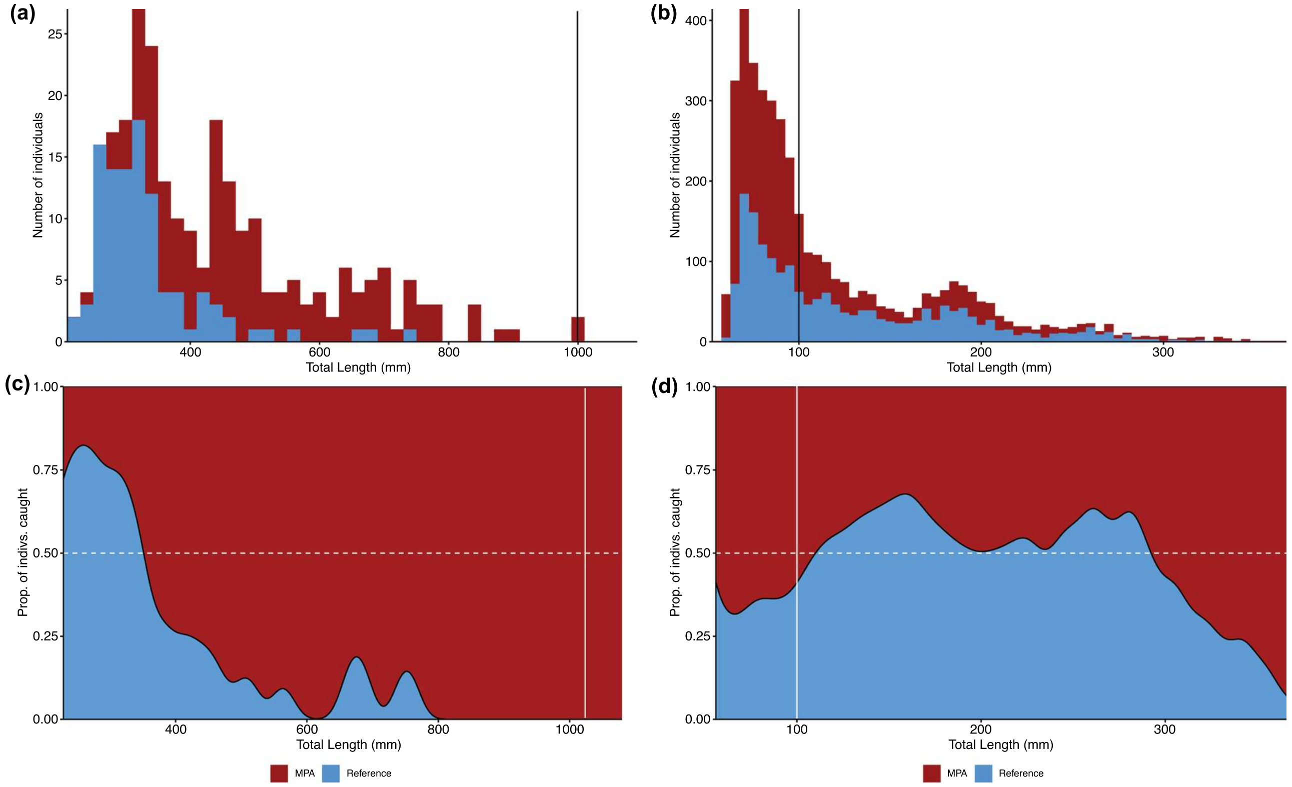

FIGURE 5 Leopard sharks (*Triakis semifasciata*) (247 fish, all juveniles) and barred surfperch (*Amphistichus argenteus*) (4096 fish, 2856 juveniles, and 1240 adults) observed in beach seines in marine protected areas (MPAs) and reference sites across all regions combined: (a) total length (TL) of all leopard shark individuals, (b) TL of all barred surfperch individuals, (c) proportion of leopard sharks individuals by TL (148 inside MPA, 98 in reference sites), and (d) proportion of barred surfperch individuals by TL (2294 in MPA, 1840 in reference sites) (horizontal dashed lines, 50:50 ratio of adults and juveniles; solid vertical lines, size limit for juveniles of each species [leopard shark TL < 1000 mm; barred surfperch TL < 100 mm]).

DISCUSSION

We assessed the effects of MPAs on surf zone fish assemblages over a broad biogeographical scale. Our work represents the first such comprehensive analysis in the eastern Pacific and specifically in California's MPA network. In MPAs, we observed higher abundance, richness, and biomass of surf zone fish (Figure 3) than in reference sites. However, we only observed these MPA effects in the south region, and these effects were contingent on the survey method employed. Specifically, BRUV surveys in the south region yielded higher abundance and richness inside MPAs, whereas these metrics yielded similar results inside and outside MPAs in seine surveys (Figure 3; Appendix S9). We observed higher biomass in seines inside MPAs in the south region but in no other regions (Figure 3). Seine survey results indicated high variability in metrics across the MPA network; site pair contributed to a large amount of this variation (Table 1). However, for BRUVs, a stronger influence of MPA and region was evident (Table 1). Region also played a crucial role in MPA performance, with the south region showing the largest effect size among the tested predictors (Figure 6). Together these results underscore the pivotal role of MPA location (region and site pair) in measuring MPA performance.

Our results for the south region indicated positive MPA effects for all of our metrics. In the south region, there were significantly higher fish abundance and richness in BRUVs and biomass in seines inside MPAs. Studies of multiple habitats in California's MPA network emphasize this region's role in network-wide MPA effects (Caselle et al., 2023; Ziegler et al., 2024). Previous research in nearshore subtidal rocky reefs in which BRUVs (Jaco & Steele, 2020a) and underwater visual censuses (Caselle et al., 2015; Hamilton et al., 2010) were used showed that targeted species exhibit rapid responses to MPA protection in southern California (<5 years following MPA establishment). Specifically, these studies showed that targeted species are more abundant, larger in size, and higher in biomass inside MPAs. In contrast, MPA effects appear to develop more slowly in northern regions (Starr et al., 2015; Ziegler et al., 2024), where fishing pressure is less intensive due to reduced accessibility and reduced human population density (Free et al., 2023). Physical characteristics may also play a role in the detection of MPA impacts (Edgar et al., 2014; Hamilton et al., 2010). Warmer SST and lower wave heights, factors known to influence surf zone fish communities (Clark et al., 1996; Favero & Dias, 2013; Pattrick & Strydom, 2014), are typical of the south region of California (Appendices S3 & S4). This regional variation in temperature can influence biogeographical patterns of

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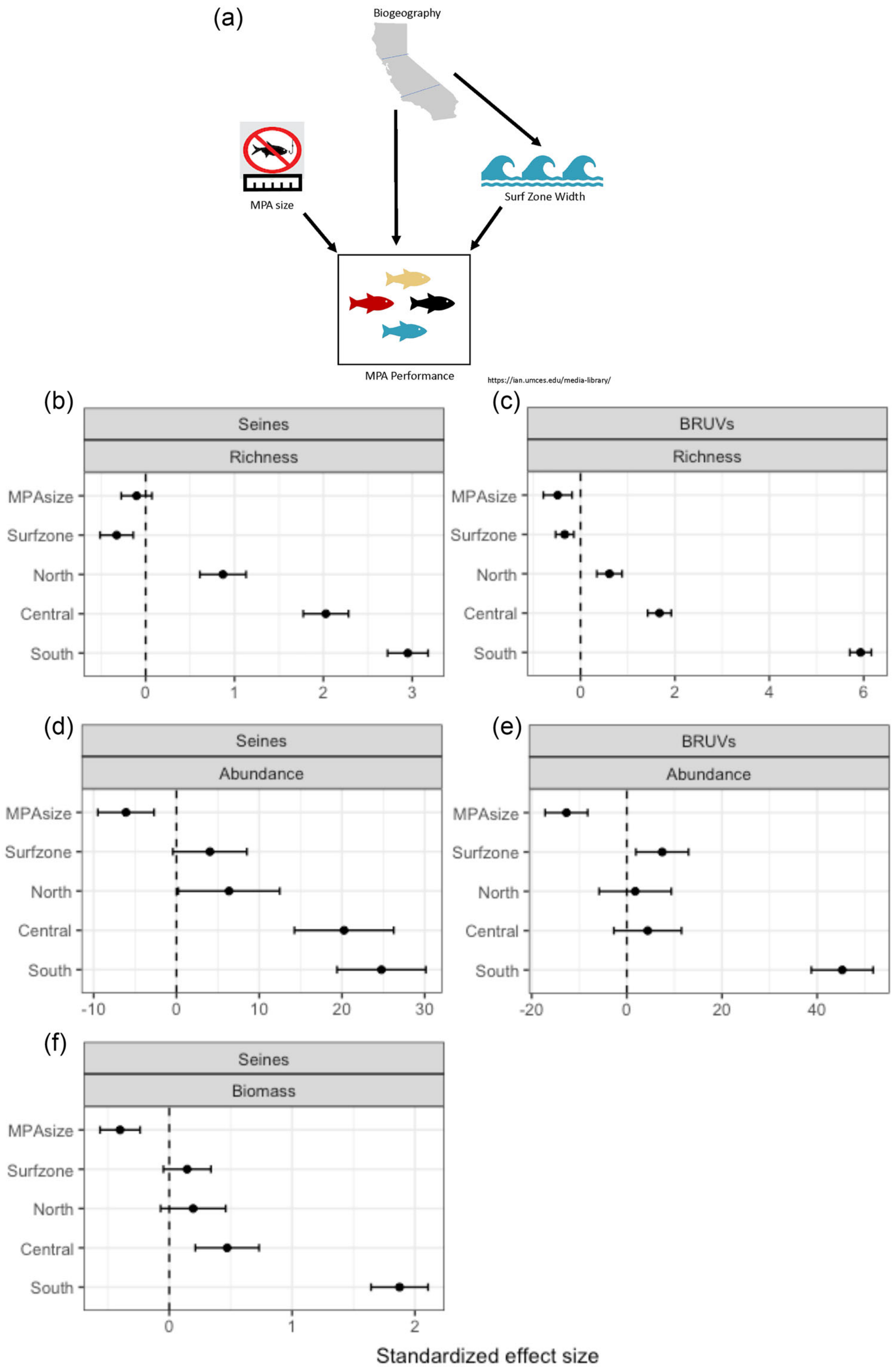

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FIGURE 6 (a) Casual relationships of marine protected area (MPA) size, surf zone width, and biogeography on MPA performance and standardized effect sizes for the 3 predictors on species richness per unit effort (RPUE) in (b) seine surveys and (c) baited remote underwater video camera (BRUV) surveys, (d) catch per unit effort (CPUE) (abundance) in seine surveys, (e) maximum number (MaxN) per unit effort (abundance) in BRUV surveys, and (f) biomass per unit effort (BPUE) in seine surveys. The *x*-axes scale with the response variable.

species ranges (Horn & Allen, 1978; Miller, 2023), and shifts in species composition among bioregions could help explain the stronger signal of MPAs in the south compared with other regions because MPA protection can affect species and taxa differently (Molloy et al., 2009; Tetreault & Ambrose, 2007). Although species targeted by fisheries are predicted to respond strongly to MPAs (Caselle et al., 2015; Hamilton et al., 2010), not all targeted fish experience the same fishing pressure. Realized

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fishing pressure on individual species combined with certain life-history traits can influence the magnitude and direction of MPA effects among species (Knott et al., 2021; Micheli et al., 2004; Molloy et al., 2009; Pinnegar et al., 2000).

Our main biological metrics focused on differences of the surf zone fish community as a whole inside and outside MPAs. This inherently averages responses among many species with distinct fishing pressures and life-history strategies, and this approach might obscure certain effects. For example, our analysis of surfperch family (Embiotocidae) as a whole showed no difference in biological metrics inside and outside MPAs (Figure 4), whereas barred surfperch (one of the most highly targeted species by shore anglers) exhibited significant variation in size structure inside and outside MPAs (Figure 5d). Moreover, our study revealed significantly higher species richness in the south region compared with both the central and north regions for both survey methods. In seine surveys, we observed approximately twice the species richness in the central and south regions compared with the north region. The higher species richness in the south region could increase the probability of including species more likely to show MPA effects (Blowes et al., 2020). For example, the community composition in the south region was distinct from the other 2 regions and was characterized by a higher relative abundance of more southern California species (Horn & Allen, 1978; Miller, 2023), including California corbina and other croakers (Sciaenidae), Elasmobranchs, and barred surfperch (Figure 2). These targeted fish species are expected to show benefits of MPA protection due to their popularity among recreational shore fishers (Jaco & Steele, 2020b; Schroeder & Love, 2002).

Despite sharing certain life-history traits expected to enhance MPA effects and past fishing pressures, elasmobranchs and surfperch exhibited contrasting MPA effects. In the south region, where they were most abundant, elasmobranchs as a group demonstrated a strong influence of MPAs (Figure 4). Although many elasmobranchs are considered highly mobile and have large home ranges (Block et al., 2011; Heupel et al., 2004; Skomal et al., 2009), the species prevalent in our study display seasonal migrations with prolonged periods of reduced mobility linked to their reproductive cycle (Carlisle & Starr, 2009; Launer, 2014). If these periods of reduced seasonal mobility occur inside MPAs, even species categorized as highly migratory may experience higher survival in response to spatial protections from fishing (Dwyer et al., 2020; Speed et al., 2010). In the south region, we observed significantly higher biomass of elasmobranchs in seines and 65% greater MaxN on BRUVs inside MPAs compared with reference sites (Figure 4). We also observed a greater proportion of larger juvenile leopard sharks inside MPAs (Figure 5c). This live bearing species is both commercially and recreationally fished in California (Kusher et al., 1992; Smith, 1990). Leopard sharks exhibit site fidelity (Norse, 2010; Nosal et al., 2013); however, there is evidence that a small proportion of leopard sharks in California can disperse a great distance (Smith, 1990). The high abundance of juvenile leopard sharks (Figure 5a,c) inside MPAs in our seine surveys highlights the role of surf zones as important juvenile habitat and the potential importance of MPAs for this species (Escalle et al., 2015; MacKeracher et al., 2019). In contrast to elasmobranchs, overall abundance and biomass of surfperch did not differ inside and outside MPAs (Figure 4). However, population size structure for barred surfperch, a recreationally targeted species, reflected an MPA signal numbers of large adult and small juvenile fish were higher in MPAs than in reference sites (Figure 5d). A second species of targeted surfperch, silver surfperch, also showed similar patterns of higher abundance of larger adults and smaller juveniles in MPAs compared with reference sites (Dugan et al., 2022). These results suggest that MPA effects for some species can potentially include a wider range of body sizes that reflect the fecundity of large mature viviparous fish inside an MPA, rather than just larger sized fish overall. Although many of the species we observed are targeted by shore fishers, comprehensive records and estimates of the degree of fishing pressure these species experience are lacking. Understanding how relative fishing pressure affects differences inside and outside MPAs for these species should be investigated in future studies because our results (like others) suggest that relative fishing pressure and life-history traits need to be incorporated into conservation goals and planning (Jennings et al., 1999; Mann et al., 2016).

The ecological success of MPAs can be influenced by a variety of environmental and anthropogenic factors (Edgar et al., 2014). Despite the small size of MPAs studied here (Appendix S2), we observed benefits to surf zone fish populations inside MPAs in the south region, consistent with studies of other habitats in the California MPA network (Caselle et al., 2023; Tetreault & Ambrose, 2007; Ziegler et al., 2024). In our analysis of factors affecting MPA performance, we found that MPA effects, in terms of abundance and biomass, were highest in smaller MPAs with wide surf zones (Figure 6b–f). In contrast, the most speciose MPAs had narrow surf zones (Figure 6b–f), potentially implying proximity to adjacent habitats, such as rocky reefs, influences patterns of diversity. This indication of the importance of habitat connectivity is consistent with previous studies on marine reserves in Australia (Ortodossi et al., 2019) that show that reserves connected to adjacent fish habitats (within 100 m of rocky headlands) support a greater diversity of surf zone fish. However, our findings for MPA size (length of protected shoreline) contradict previous findings for surf zone fish that report the benefits of large reserves (>1.5 km of beach frontage [Ortodossi et al., 2019]). Some studies also report minimal effects of MPA size (Côté et al., 2001; Guidetti & Sala, 2007; Halpern, 2003), whereas others demonstrate that the effects of protection from fishing are stronger in larger MPAs (Claudet et al., 2008), including those in deeper rocky habitats in California (Ziegler et al., 2024). Instead, we observed that the influence of region overshadowed the influences of MPA characteristics and habitat availability for surf zone fish ecosystems in California. Our findings suggest that for conservation of surf zone fish, managers should consider the influence of biogeographic region on MPA performance (Figure 6).

In the first assessment of surf zone fish inside MPAs on open-coast beaches over a broad latitudinal range in the northeast Pacific, our results highlight the multifaceted effects of MPAs on the surf zone fish community. Overall, our findings

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suggest that MPAs can be a valuable management tool for safeguarding vulnerable surf zone fish; however, the detection of these MPA effects was limited to the south region and varied with survey method. For MPA performance, region generated much greater effect sizes than MPA size and surf zone width with much larger effects detected for the south region. We conclude that regional differences in species richness and composition, combined with differences in surf zone fish assemblages observed by our 2 survey methods, contributed to the variation in MPA effects we observed across our different biological metrics and study site pairs. More research on surf zone fish is warranted to illuminate factors (differences in fishing pressure, environment, etc.) driving effects of MPAs for these highly accessible and exploited, yet understudied, ecosystems. It is crucial for managers to consider specific taxa, their biogeographical distribution, and microhabitat characteristics when designing and evaluating MPAs for surf zone fish because these factors can influence both MPA performance and detection of MPA effects. Although we focused on MPAs in California's network, our results illustrate how biological metrics, survey methods, biogeography, and taxa of interest can affect estimates of MPA success.

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This article has earned an Open Data badge for making publicly available the digitally-shareable data necessary to reproduce the reported results. The data is available at https://search.dataone.org/view/urn%3Auuid%3Addf212bf-91d6-4c0d-b5ef-c53951cfa218urn:uuid:ddf212bf-91d6-4c0d-b5ef-c53951cfa218. Code for this project can be found at https://github.com/Marraffini/MS_surfzone.git

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