



Effects of marine reserves on predator–prey interactions in central California kelp forests

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ABSTRACT: Marine reserves are often designed to increase density, biomass, size structure, and biodiversity by prohibiting extractive activities. However, the recovery of predators following the establishment of marine reserves and the consequent cessation of fishing may have indirect negative effects on prey populations by increasing prey mortality. We coupled field surveys with empirical predation assays (i.e. tethering experiments) inside and outside of 3 no-take marine reserves in kelp forests along the central California coast to quantify the strength of interactions between predatory fishes and their crustacean prey. Results indicated elevated densities and biomass of invertebrate predators inside marine reserves compared to nearby fished sites, but no significant differences in prey densities. The increased abundance of predators inside marine reserves translated to a significant increase in mortality of 2 species of decapod crustaceans, the dock shrimp *Pandalus danae* and the cryptic kelp crab *Pugettia richii*, in tethering experiments. Shrimp mortality rates were 4.6 times greater, while crab mortality rates were 7 times greater inside reserves. For both prey species, the time to 50% mortality was negatively associated with the density and biomass of invertebrate predators (i.e. higher mortality rates where predators were more abundant). Video analyses indicated that macro-invertivore fishes arrived 2 times faster to tethering arrays at sites inside marine reserves and began attacking tethered prey more rapidly. The results indicate that marine reserves can have direct and indirect effects on predators and their prey, respectively, and highlight the importance of considering species interactions in making management decisions.

KEY WORDS: Marine reserve · Trophic ecology · Indirect effects · Mortality · Decapoda · Crabs · Shrimp · Fish · Rockfish

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1. INTRODUCTION

Predation is a fundamental process that structures ecological communities and shapes their function. Predators serve to regulate prey abundance through direct consumptive effects (Murdoch 1969) and to alter prey behavior through indirect non-consumptive effects (Schmitz et al. 1997, Madin et al. 2010). Predators are especially important in marine ecosystems (Tegner & Dayton 2000) and are responsible for preserving community diversity on temperate and

tropical reefs (Paine 1966, Hughes 1994, Williams & Polunin 2001, Mumby et al. 2006). The development of the keystone species paradigm occurred in marine systems, illustrating how predators can disproportionately affect prey diversity by consuming the dominant competitor (Paine 1969), and can prevent dramatic phase shifts by regulating the abundance and behavior of grazers (Estes & Duggins 1995). Over the last 50 yr or so, the urgency of understanding the ecological effects of predators in marine communities has intensified due to their overexploitation. Cen-

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turies of fishing have removed once prominent populations of large, predatory fishes from most marine ecosystems (Pauly et al. 1998, Myers & Worm 2003, Estes et al. 2011). Fisheries catch data reflect the tendency to first target species at higher trophic levels before subsequently targeting species at lower trophic levels (Pauly et al. 1998, Essington et al. 2006). Despite the difficulty in studying predators due to their large sizes and extensive home ranges, a multitude of case studies over a variety of spatial scales have demonstrated that when predators are removed or reduced in a system, adverse negative effects often occur (Estes et al. 2011).

Management measures that stimulate predator recovery in marine environments can potentially reverse the effects of predator removal in these systems. Options range from single-species fisheries regulations (e.g. catch limits or size limits) to ecosystem-based management strategies, such as Marine Protected Areas (MPAs), that can limit fishing activities more broadly. No-take marine reserves are a type of MPA where all extractive activities are prohibited, protecting the entire ecosystem. Recently, more attention has been paid to evaluating the effectiveness of marine reserves and to understanding the timescales of recovery based on MPA age, fishing pressure, and species-specific life history characteristics (Kaplan et al. 2019, Nickols et al. 2019). Evidence from around the globe demonstrates positive direct effects of marine reserves on the size of individuals, density, biomass, and diversity of predatory fish populations inside their boundaries (Halpern & Warner 2002, Lester et al. 2009). Predator behavior may also be altered by marine reserve protection, as predators are bolder and exhibit less risk averse behavior inside reserves compared to nearby fished sites (Rhoades et al. 2018, 2019). Often, the direct effects of marine reserve protection are strongest on species targeted by fishing activities (Hamilton et al. 2010, Caselle et al. 2015). Because many targeted species are higher trophic level predators, rapid recovery of predators may trigger changes in lower trophic levels through increased consumption of prey species (Graham et al. 2003, Micheli et al. 2004), as has been documented in many MPA locations where sea urchins are prey (McClanahan & Muthiga 1989, Sala & Zabala 1996, Shears & Babcock 2002, Guidetti 2006, Pederson & Johnson 2006, Ling et al. 2009). These indirect negative effects of marine reserves on lower trophic levels may take a decade or longer to propagate through the food web (Babcock et al. 2010) and depend on whether the prey species are also harvested (Shears et al. 2012). Marine reserves may

also enhance trophic redundancy by preserving multiple predator species and can thereby stabilize ecosystem dynamics and promote resilience (Eisaguirre et al. 2020).

Observing predator–prey interactions and estimating prey mortality rates in the field can be challenging, especially in situations where visibility is poor and prey are small and cryptic. Tethering is a useful technique that can serve as a proxy for predation risk. This technique has been utilized in many marine systems, often to quantify prey mortality in response to management measures such as marine protection (McClanahan & Muthiga 1989, Aronson & Heck 1995, Sala & Zabala 1996, McClanahan 1999, Shears & Babcock 2002, Guidetti 2006, Pederson & Johnson 2006, Ling et al. 2009, Loflen & Hovel 2010, Dee et al. 2012, Rhoades et al. 2019). The act of tethering can artificially elevate prey mortality rates by inhibiting the prey's natural escape response (Peterson & Black 1994, Zimmer-Faust et al. 1994, Nemeth 1997, Kneib & Scheele 2000). Tethering can also be problematic in evaluating predation rates in the field if there are different types of predators present in different habitats or treatments, and some of those predators are successful in capturing prey that would normally be able to escape (Barbeau & Scheibling 1994, Zimmer-Faust et al. 1994, Mills et al. 2008). These tethering biases can be minimized as long as experimental conditions are kept constant amongst treatments (i.e. sites), the species of predators are similar amongst treatments, and the result is not viewed as an absolute and accurate measure of the true mortality rates experienced in the field, but instead as a relative proxy of predation risk to be compared among treatments or locations (Aronson et al. 2001, Mills et al. 2008, Dee et al. 2012, Ory et al. 2014).

In central California kelp forests, the giant kelp *Macrocystis pyrifera* and large understory kelps dominate rocky reefs and provide habitat for myriad predatory fishes and their invertebrate prey (e.g. Schiel & Foster 2015). These predatory fishes are commonly targeted by fishing activities. In this region, a statewide network of MPAs includes 2 well established no-take reserves (since 1973 and 1984) and several recently added MPAs (protected since 2007). Prior evaluations of these reserves and other long-term closed areas in central California revealed positive effects on the abundances and size structure of certain predatory fishes inside their boundaries (Paddock & Estes 2000, Marks et al. 2015, Starr et al. 2015), providing signs of predator recovery in some locations following the cessation of fishing. Similar recoveries in southern California (Hamilton et al.

2010) and tropical reef systems (Soler et al. 2015) span multiple trophic levels, and the diversity of predatory fish functional groups in central California offers an opportunity to investigate these effects in a different system. Spatial variation in predator abundance created by the network of marine reserves provides an ideal setting to empirically test how predatory fish may influence prey populations when habitat complexity is similar but predation pressure differs.

The primary question addressed by this study was whether predator recovery has occurred in central California marine reserves, and how prey populations and mortality are associated with spatial differences in predator abundance between reserve and fished sites. In order to answer this question, we designed experiments that quantified survival rates of tethered invertebrates between marine reserves and adjacent fished sites, utilizing (1) SCUBA surveys to test for differences in fish and invertebrate abundances to establish treatment conditions; (2) field predation trials quantifying relative survival rates of 2 invertebrate prey species; and (3) underwater camera recordings to provide data on predator identity, relative abundance, and predator–prey interactions. We hypothesized that density and biomass of fishes that consume invertebrates (i.e. invertivores) would be greater inside reserves compared to fished sites. We predicted that prey species, specifically crustaceans, would be less abundant inside reserves due to higher predation rates. We also hypothesized that survival of tethered crabs and shrimp would be lower inside reserves and the elapsed time until the arrival of the first potential predators to tethering assays would be faster inside reserves, where predatory fishes are more abundant and exhibit less risk averse behavior due to protection from fishing. Finally, we hypothesized that the number of predatory strikes on crustacean prey would be greatest for macro-invertivore predators, compared to other predator functional groups, due to a better pairing of prey size and predator gape (i.e. mouth size).

2. MATERIALS AND METHODS

2.1. Study sites and species

The study area off the central coast of California, in Monterey and Carmel Bays, is characterized by heterogeneous

rocky reef habitat comprised of large slabs of granitic bedrock divided by areas of large boulders, intermittent cobble, and patches of sand. The major primary producer, *Macrocystis pyrifera*, grows dense during the summer season, creating kelp forests that provide food and shelter to support the subtidal community (Schiel & Foster 2015). These kelp forests include understory kelps, a benthic community of articulated and encrusting coralline algae, many species of fleshy red and brown macroalgae, and a highly diverse temperate community of sessile and mobile invertebrates (Hines 1982, Schiel & Foster 2015).

Six sites were used in 2014 and 2015 (Fig. 1): 3 in state marine reserves (SMRs, no-take MPAs, hereafter 'reserve sites'), and 3 in state marine conservation areas (SMCAs, hereafter 'fished sites') that permit the take of finfish and kelp harvesting. Each reserve site had an associated fished site that served as a reference. A fourth fished site, Otter Point, was used for a crab predation assay and visual fish surveys in 2014 only (Fig. 1). The reserve sites and their years of establishment are as follows: (1) Point Lobos SMR, all fishing prohibited since 1973, (2) Hopkins Marine Life Refuge (recently changed to Lovers Point–Julia Platt SMR), all fishing prohibited since 1984, and (3) Carmel Pinnacles SMR, all fishing prohibited since 2007. Established in 2007, the fished sites, in order of their adjacent reserves, respectively, are (1) Butterfly House, (2) Otter Point and McAbee Beach, and (3) Stillwater Cove. Two of the fished sites, Butterfly

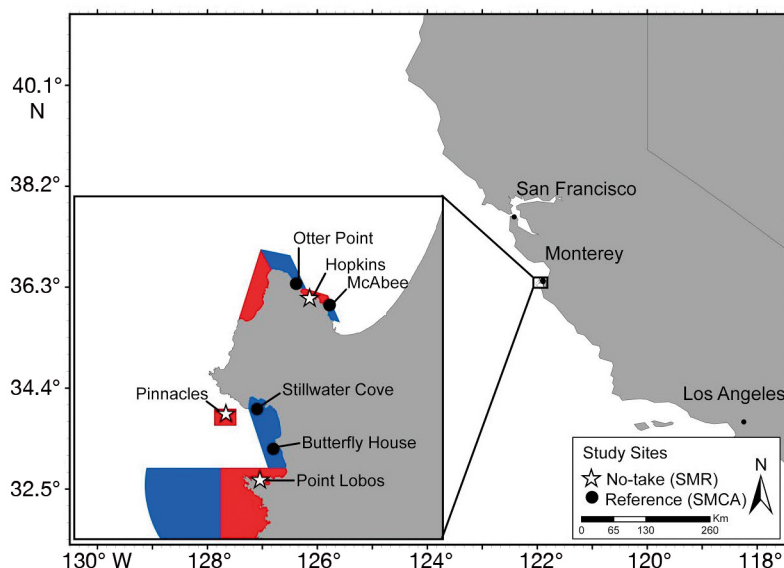


Fig. 1. Study sites in southern Monterey Bay (Otter Point, Hopkins, and McAbee) and Carmel Bay. (Red areas) No-take state marine reserves (SMRs; reserves) and (blue areas) state marine conservation areas (SMCAs; fished sites) that allow recreational take of finfish

House and Stillwater Cove, fall within the Carmel Bay SMCA, while Otter Point (Pacific Grove Marine Gardens SMCA) and McAbee Beach (Edward F. Ricketts SMCA) lie to either side of the Lovers Point–Julia Platt SMR (Fig. 1).

The main predatory fishes in these kelp forests consist of omnivorous rockfishes *Sebastes* spp. (Rosenthal et al. 1988), carnivorous cabezon *Scorpaenichthys marmoratus* (Hart 1973), kelp greenling *Hexagrammos decagrammus* (Armstrong 1996), surfperches *Embiotoca* spp., and piscivorous lingcod *Ophiodon elongatus* (Clemens & Wilby 1961). For several analyses, predatory fishes were categorized into 4 functional groups based on their primary dietary habitats (Love 2011): macro-invertivore, micro-invertivore, piscivore, or planktivore (Clemens & Wilby 1961, Hart 1973, Nemeth 1997, Micheli & Halpern 2005; see Table S1 in the Supplement at www.int-res.com/articles/suppl/m655p139_supp.pdf). Macro-invertivores and micro-invertivores (referred to as invertebrate predators when combined) were separated based on differences in the size of the typical invertebrate prey consumed as described in published resources. Both groups are capable of consuming smaller prey, while micro-invertivores can become gape-limited and unable to prey on larger invertebrates. We predicted that these distinctions could affect strike and predator success rates during tethered prey assays.

Two species of decapod crustaceans, the cryptic kelp crab *Pugettia richii* and the dock shrimp *Pandalus danae*, were selected as prey species to test for spatial differences in relative survivorship among marine reserve and fished sites. *P. richii* are detritivores, feeding mainly on drift kelp of *M. pyrifera*. This species of Brachyuran spider crab is commonly found in kelp beds in central California, where they are an important food source for several kelp forest predators, including many species of fish (Hines 1982). *P. danae* are benthic omnivores, feeding on small crustaceans, mysids, and detritus (Butler 1964, Neilson 1981). These Pandalid shrimp are commonly found in cracks in rocks, and in coarse sandy areas in and near kelp beds and breakwaters, serving as a food source for numerous fishes, including flatfishes, lingcod, and rockfishes (Hart 1973, Neilson 1981).

2.2. Survey techniques

Underwater visual surveys were completed to assess whether reserve sites had higher abundances of predatory fishes than adjacent fished sites. At all 7

sites, divers counted and estimated the total length (to the nearest 1 cm) of all demersal fishes occurring within 2 m of the benthos along four 2 × 30 m belt transects placed at the inner (nearshore) and outer (offshore) edge of the kelp forest. Transects in these 2 zones were completed during the summers of 2014 and 2015, for a total of 16 fish transects at each site, except at Otter Point, where transects were only conducted in 2014. Fish density was calculated by dividing the counts on each transect by the area of bottom surveyed (i.e. 60 m²). Divers estimated total lengths of fishes during surveys, which were converted to weights using species-specific conversions (weight = $a \times \text{length}^b$, where a and b are species-specific constants) (Froese & Pauly 2019). Weights of each species per transect were divided by 60 m² to calculate the biomass density (g m⁻²). For subsequent analyses, species were placed into the 4 predatory functional groups described in Section 2.1.

Divers conducted specialized surveys to assess whether densities of invertebrate prey, specifically crabs and shrimp, differed among reserve and fished sites. Different techniques were employed in 2014 and 2015. In 2014, a 60 m transect was laid in both zones (inner and outer edge of the kelp forest) at all 7 sites, and 0.25 m² quadrats were placed every 4 m along the line ($n = 15$ points per transect). Each quadrat was searched for crabs and shrimp by each diver independently and the 2 counts were averaged at that point on the transect. In 2015, targeted 'crevice' surveys were employed to focus searches on the microhabitat occupied by small crabs and shrimp in our study system. Six 10 m segments along a 60 m transect were sampled in both zones at 6 sites (excluding Otter Point). Within each 10 m segment, divers haphazardly selected 1 crack or crevice bisected by the meter tape and counted all decapod crustaceans inside a 1 × 0.05 m search area. Divers used flashlights to look for crustaceans inside cracks and crevices. Variation in the dimensions of cracks and crevices, as well as growth obstructing the opening, hindered the ability of divers to completely view these microhabitats. Therefore, divers only quantified crabs and shrimp present in the initial 50 cm of a crevice, which was always visible. At each site, 12 crevice surveys were completed during summer 2015.

2.3. Predation assays

Standardized tethering assays were deployed at each site to examine whether survivorship of invertebrate prey differed between reserve and fished sites.

Each tethering assay involved (1) collection of specimens, (2) tethering of specimens in the laboratory, and (3) field deployment. During collections, divers caught crabs by hand, and shrimp were herded out of small crevices using a blunt-ended dive knife. Collections occurred in the Monterey Bay Harbor, at 36°36'16.4" N, 121°53'29.0" W, where both species were more abundant and easier to capture than in nearby kelp beds (D. C. Yates pers. obs.). Collected organisms were held in constant-flow seawater tanks in a laboratory at Moss Landing Marine Laboratories (MLML), tethered using the procedures described below, and carefully observed for at least 24 h before deployment to watch for any deleterious effects resulting from the tethering process. Laboratory experiments were conducted to develop tethering methods for the field. Ideal tether lengths were 20 cm, which allowed the organisms to retain moderate mobility, while minimizing entanglement. Crabs were tethered using 60 pound test Spectra braided fishing line, tied into a lasso around their carapace, with a dot of cyanoacrylate adhesive to hold the knot in place, and a 20 cm extension of the lasso to attach them to the substrate (Loflen & Hovel 2010). The line strength and tether design were sufficient to prevent crabs from escaping (no crabs escaped their tethers in 8 d of laboratory trials). Shrimp were tethered using a dot of cyanoacrylate adhesive to attach a 20 cm length of 6 pound monofilament on the upper part of their dorsum (Pirtle et al. 2012). This tether design was also sufficient to prevent escape (no shrimp escaped their tethers in 7 d of laboratory trials). To permit tracking of mortality as a function of prey size, each tethered organism was labeled with a unique identification number printed on a self-adhesive piece of plastic tape. Lengths of each crab were recorded as the distance (mm) from tip of the rostrum to the furthest point on the abdomen. Shrimp lengths were recorded as the distance (mm) from the tip of rostrum to the furthest point on the uropod when extended.

Prior to deploying the predation assays, divers at each of the 7 sites scouted for large, suitable areas either of flat bedrock or large boulders at depths of 8 to 14 m. Care was taken to select similar habitat characteristics for deployment, in an effort to minimize how microhabitat differences may influence predator foraging or prey sheltering behavior. A tethering array consisted of prey tethered to 0.95 cm (3/8 inch) thick galvanized chain laid out in rows on the reef bottom, and cameras mounted on 0.5 m lengths of PVC attached vertically to concrete blocks. Tethered prey were transported in individual seawater-filled plastic containers to dive sites and attached to links

of the chain with cable ties. For crab trials, 2 m lengths of chain were laid on the reef and arranged in 12 parallel rows, spaced 0.5 m apart. Divers attached tethered crabs at 50 cm intervals, with 5 individuals per 2 m chain, and 60 total crabs per trial at a site (see Fig. S1 in the Supplement). Four video cameras were placed at the corner of each crab array and oriented to capture all crabs and their potential predators within the camera frame. For shrimp trials, shrimp were separated into 6 replicate groups of 10 individuals at each site, and each group spaced 10 to 15 m apart to reduce the potential for 1 predator to locate and consume all 60 prey. Lengths of chain 2 m long were laid parallel to one another, spaced 0.5 m apart, and 5 tethered shrimp were attached to each chain at 0.5 m intervals. High definition underwater video cameras (GoPro Hero3) were placed at one end of each replicate chain, capturing all 10 tethered prey within the frame (Fig. S1), recording up to 4 h of continuous video per day.

In order to track survival, divers revisited tethering assays every 24 h during crab trials and at 0.5, 1, 3, 7, and 24 h intervals during shrimp trials. During each diver census, every tether was examined, individual identification numbers noted, and the status of each crab or shrimp was recorded as 'alive', 'missing', or 'dead'. In order to prevent sea star predation and isolate the effects of fish predation on crustacean prey, all sea stars (*Dermasterias imbricata*, *Patiria miniata*, *Pisaster giganteus*, *Pycnopodia helianthoides*) were collected in mesh bags within a 10 m radius from the site and released 30 m from the tethering assay. Predation trials ran until fewer than 3 tethered crabs or shrimp remained, or until they reached the cutoff time, which was set at 168 h for crabs, and 48 h for shrimp. Crab trials were conducted at all 7 sites in summer 2014, and shrimp trials were conducted at 6 sites, excluding Otter Point, in summer 2015.

Predation events that were observed on video were integrated into survival curves in order to examine survivorship on a finer time scale than the diver census interval. Times until 50% mortality were calculated for each site. Since the time at 50% mortality frequently occurred between diver censuses, the rate of mortality from the most recent diver census (i.e. number lost per hour) was used to estimate the time elapsed until 50% mortality was reached in that interval. To examine shifts in prey size distributions due to predator selectivity before and after the time at 50% mortality, diver censuses and the tethered prey identification numbers were related back to their individual sizes, and used to calculate size frequency distributions.

2.4. Video analysis

Interactions between tethered invertebrate prey species and potential predators were monitored using underwater GoPro cameras. With extended batteries, GoPro cameras captured, on average, 2.7 h (± 0.1 SE) of continuous footage at the start of each deployment. Video footage was analyzed in the laboratory at normal speed on a high definition television monitor. Video footage supplemented diver censuses on predation rates, and provided additional metrics with which to assess predation risk across the study region. These metrics included the timing of arrival for both predators and non-predators, relative abundance estimates of predators, and strike observations: predator identity, number and timing of strikes, and strike success or failure. Strike rate per hour was calculated from the number of observed predator attacks divided by the amount of time recorded for each replicate. These rates were averaged into successful and unsuccessful strikes per site and compared among fish functional groups and reserve status.

In order to use video footage to assess whether predators that are attracted to shrimp prey show up in greater abundance at tethering assays inside reserves, relative fish abundance was estimated using F_{\max} , the maximum number of individuals per species observed in the video frame. This is a conservative metric and ensures that individual fish were not counted multiple times (i.e. MaxN, Willis & Babcock 2000). The F_{\max} metric thus represented the minimum number of unique individuals per species present at each feeding assay. Totals of F_{\max} (i.e. summed across species) for each functional group were averaged at each site from footage from 2015 only, and compared between reserve and fished sites to estimate total predator abundance during the predation assay. To determine if predators arrived more quickly to the tethering assay inside reserves, another metric (T_{inst}) was recorded for each replicate (Willis & Babcock 2000), which represents the time it takes for the first individual of each potential predator species to enter the video frame. Average T_{inst} values were calculated for each fish functional group and compared among sites and reserve status. To examine patterns of predator visitation frequencies at tethering assays, observers stopped the video every 30 s and counted the total number of potential predators that were within 0.5 m of the assay for the first 6000 s or 1.67 h (the shortest video length) of each replicate (Willis & Babcock 2000). Those visitation frequencies were then averaged across sites and plotted by reserve status.

2.5. Statistical analyses

We conducted nested analysis of variance (ANOVA) to test whether the density and biomass of fish predators differed among the reserve and fished sites, while accounting for other potential sources of variation. Using separate statistical models for each predator functional group (i.e. macro- and micro-invertivore, piscivore, and planktivore), we tested models including the terms Year, Reserve status, Site (nested within Reserve), and Zone (nested within Site and Reserve). Year, Reserve status, and Zone (inner vs. outer edge of the kelp bed) were fixed factors in the analysis while Site was a random factor. F -ratios were adjusted for random factors by modifying the mean square term in the denominator. We tested for normality of residuals and homoscedasticity. For fish biomass, values were square root transformed prior to analysis. To test whether the abundance of invertebrate prey differed between reserve and fished sites, we used similar nested ANOVA models. However, because we used 2 different survey techniques in different years, the data could not be pooled. Therefore, we conducted separate ANOVA tests each year using the factors of Reserve status, Site (nested with Reserve), and Zone (nested within Site and Reserve). Reserve status and Zone were fixed effects, while Site was a random factor in the analysis.

We also examined correlations between invertebrate prey abundance and predator abundance, using the mean abundance of each group as our response variable. Invertebrate prey survivorship curves were compared between reserve and fished sites using Kaplan-Meier survival analysis. We used the time to 50% mortality as an additional response variable and tested for correlations between mortality rates and predator abundance across the reserve and fished sites for each predator functional group and all invertebrate predators (combining macro- and micro-invertivores). To examine whether predators exhibited selectivity for prey size, we compared the size frequency distributions of crab and shrimp prey at reserve and fished sites before the start of the experiment to the size distribution remaining after 50% mortality occurred, using a Kolmogorov-Smirnov 2-sample test.

Video analysis was used to assess whether predators were more abundant, appeared sooner to the tethering array, or differed in their strike and success rates as a function of Reserve status. This analysis was restricted to the tethered shrimp assays, because predation rates were much higher and occurred on the time scale recorded by the video. To test whether

relative abundance (F_{\max}) and the time of first arrival (T_{inst}) of predators differed between reserve and fished sites, we used nested ANOVA with the factors of Reserve status and Site (nested within Reserve status). Both factors were fixed effects because the videos occurred at the specific tethering arrays established at each site. Experiments did not occur in separate Zones or Years, so those factors were not included. We compared the strike rates among the 4 fish functional groups by Reserve status using a 2-way ANOVA. Pooling sites, we used separate 2-sample t -tests for each functional group to compare the mean number of successful vs. unsuccessful attempts per hour to consume tethered shrimp. Statistical analyses were conducted in JMP v.14.

3. RESULTS

3.1. Fish and invertebrate density and biomass trends

Predator density was significantly higher inside reserves compared to fished sites for micro-invertivores (Table 1, Fig. 2). There were no significant differences in the density of macro-invertivores, piscivores, or planktivores, but in all instances the trends were for these predator groups to be more abundant, on average, inside reserves (for trends of individual species and sites, see Fig. S2 in the Supplement). Densities inside reserves were 1.3 times higher for macro-invertivores, 1.9 times higher for micro-invertivores, 1.7 times higher for piscivores, and 1.5 times higher for planktivores (Fig. 2A). We also detected differences in other explanatory variables, such that micro-invertivores differed in density among Years (higher in 2014), piscivores differed among Sites (highest at Pinnacles), and planktivores differed among Sites (highest at Pinnacles) (Table 1; Fig. S2). Predator biomass was significantly elevated inside reserves for macro-invertivores and micro-invertivores, but not significantly dif-

ferent for piscivores or planktivores due to high variability (Table 1, Fig. 2B). Overall, biomass was 2.6 times higher for macro-invertivores, 3.8 times higher for micro-invertivores, 3.6 times higher for piscivores, and 2.4 times higher for planktivores. Other factors also explained significant variation in predator biomass: Year (highest in 2014) and Site (highest at

Table 1. Statistical model results testing for differences in the density and biomass of 4 predatory fish functional groups. Nested models include the factors Year, Reserve status, Site, and Zone. Models include the factors Year, Reserve status, Site (nested within Reserve status), and Zone (nested within Site and Reserve status). Site is a random term in the model. Replicates are individual transects conducted at each site. df: degrees of freedom; SS: sum of squares; MS_{den} : mean square term for the denominator used to calculate the F -ratio.

Significant p-values (<0.05) are given in **bold**

Model	Factor	df	SS	MS_{den}	F -ratio	p
Density						
Macro-invertivore	Year	1	0.0076	0.00085	0.90	0.34
	Reserve	1	0.0025	0.00055	4.57	0.076
	Site [Reserve] & random	7	0.0027	0.00085	0.62	0.68
	Zone [Site, Reserve]	5	0.0039	0.00085	0.65	0.71
	Error	85	0.0072			
Micro-invertivore	Year	1	0.016	0.0029	5.69	0.019
	Reserve	1	0.042	0.0035	11.93	0.016
	Site [Reserve] & random	7	0.017	0.0029	1.23	0.30
	Zone [Site, Reserve]	5	0.036	0.0029	1.81	0.097
	Error	85	0.024			
Piscivore	Year	1	0.0032	0.0014	2.24	0.14
	Reserve	1	0.022	0.0086	2.52	0.17
	Site [Reserve] & random	7	0.045	0.0014	6.27	<0.0001
	Zone [Site, Reserve]	5	0.0077	0.0014	0.77	0.62
	Error	85	0.12			
Planktivore	Year	1	0.018	0.020	0.91	0.34
	Reserve	1	0.16	0.089	1.76	0.24
	Site [Reserve] & random	7	0.47	0.020	4.75	0.0007
	Zone [Site, Reserve]	5	0.27	0.020	1.97	0.067
	Error	85	1.67			
Biomass						
Macro-invertivore	Year	1	0.007	2.80	0.003	0.95
	Reserve	1	21.12	2.04	10.31	0.019
	Site [Reserve] & random	5	2.00	2.80	0.72	0.61
	Zone [Site, Reserve]	7	4.45	2.80	1.59	0.15
	Error	93	260.52			
Micro-invertivore	Year	1	5.63	1.08	5.20	0.025
	Reserve	1	56.48	4.07	13.89	0.013
	Site [Reserve] & random	5	21.15	1.08	3.91	0.0029
	Zone [Site, Reserve]	7	5.75	1.08	0.76	0.63
	Error	93	100.66			
Piscivore	Year	1	8.99	8.03	1.12	0.29
	Reserve	1	240.09	78.62	3.05	0.14
	Site [Reserve] & random	5	412.39	8.03	10.26	<0.0001
	Zone [Site, Reserve]	7	14.13	8.03	0.25	0.97
	Error	93	747.23			
Planktivore	Year	1	3.31	0.96	3.43	0.07
	Reserve	1	13.86	4.12	3.29	0.13
	Site [Reserve] & random	5	21.95	0.96	4.55	0.009
	Zone [Site, Reserve]	7	19.51	0.96	2.89	0.0009
	Error	93	89.65			

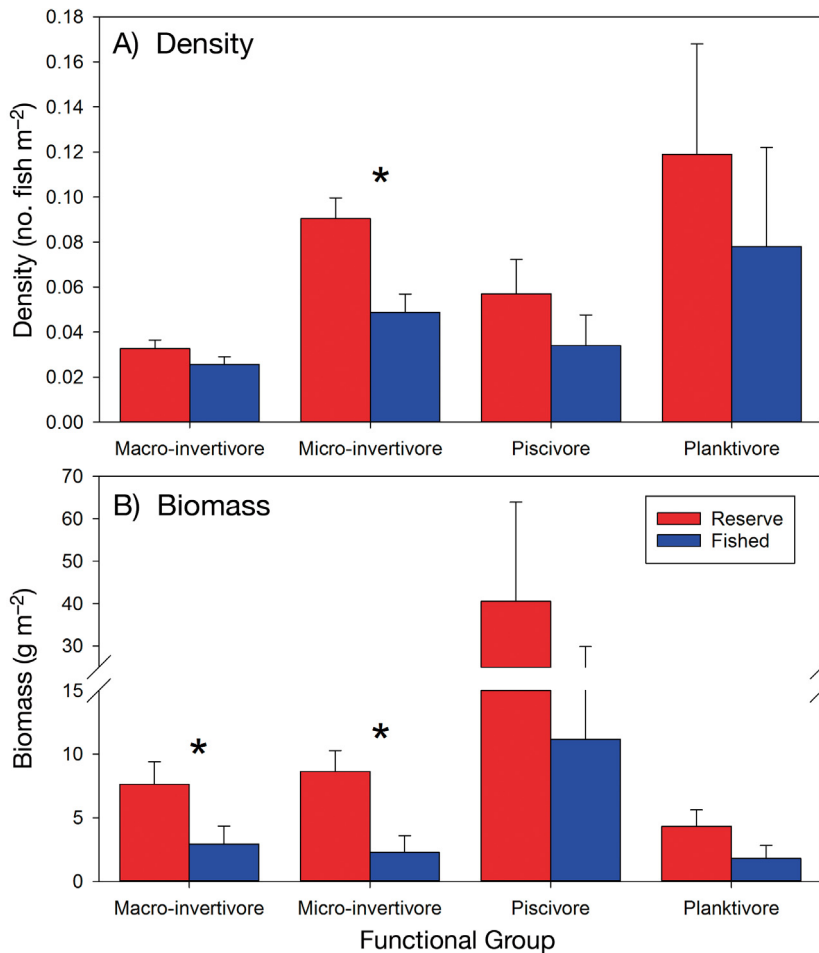


Fig. 2. Density and biomass of fishes by reserve status. Shown are the mean densities (A) and biomass (B) of each functional group (± 1 SE) calculated from diver surveys in 2014 and 2015. *Significant difference between reserve and fished sites ($p < 0.05$) in statistical models (see Table 1)

Hopkins) for micro-invertivores, Site for piscivores and planktivores (both highest at Pinnacles), and Zone (highest in Outer transects) for planktivores (Table 1; Fig. S2). Overall, the patterns indicated that invertebrate predators were more abundant, particularly in biomass, at the reserve sites compared to the fished sites at the time we conducted the tethering experiments to quantify prey survivorship as a function of reserve status.

Background crab and shrimp densities did not differ as a function of Reserve status using either the random quadrat sampling technique in 2014 or the more targeted crevice survey in 2015 (Table 2, Fig. S3 in the Supplement). We also did not detect any significant associations between the abundance of any of the predator functional groups and crab or shrimp densities in any of the surveys (Table S2, Fig. S3), although in most instances the non-significant trend

was for a negative correlation with shrimp densities being lowest in locations where predator density was highest (most so for macro-invertivores). Invertebrate prey densities did differ significantly in response to the other explanatory factors included in the statistical models. In 2014 quadrat surveys, crabs differed among Sites (highest at Point Lobos) and Zones (highest on outer transects), while shrimp differed in density among Sites (highest at Otter Point and McAbee; Fig. S3). In the 2015 crevice surveys, we only detected differences in shrimp density among Sites (highest at McAbee and Hopkins; Fig. S3). In general, shrimp were more abundant at sites in Monterey Bay than Carmel Bay (see map in Fig. 1).

3.2. Tethering experiments to quantify prey survivorship at reserve vs. fished sites

There was a clear and significant effect of reserves on crab survival (Kaplan-Meier survivability, $\chi^2 = 97.24$, $p < 0.0001$; Fig. 3A). After 24 h, only $56 \pm 4\%$ (mean \pm SE) of crabs survived inside reserves, compared to $84 \pm 2\%$ remaining alive at fished sites. By the end of the experiment (168 h), less than $1 \pm 1\%$ of crabs survived inside reserves, compared to $43 \pm 1\%$ survivorship of those tethered at fished sites.

On average for tethered crabs, the time to reach 50% mortality was 7 times longer at fished sites and there was a significant negative association between the time to 50% mortality and the density and biomass of macro-invertivore predators (Table 3, Fig. 3B,C). In addition, there were negative correlations between the time to 50% mortality and predator abundance for all predator groups, such that mortality was highest at the sites with higher predator density and biomass (Table 3). Individual survival curves for each site indicate that crabs were consumed more rapidly inside reserves compared to fished sites, except at Stillwater Cove, a fished site that experienced high mortality on par with reserve sites (Fig. S4 in the Supplement). No shifts in size–frequency distributions of tethered crabs were detected throughout the experiment, indicating that predators randomly consumed prey of

Table 2. Statistical model results testing for differences in the density of invertebrate prey across the study locations. Models include the factors Reserve status, Site (nested within Reserve status), and Zone (nested within Site and Reserve status) for 2 different types of surveys conducted separately in 2014 and 2015. Site is a random term in the model. Replicates at each site are individual 0.25 m² quadrats in 2014 and 1 × 0.05 m crevice surveys in 2015. MS_{den}: mean square term for the denominator used to calculate the *F*-ratio. Significant *p*-values (<0.05) are given in **bold**

Model	Factor	df	SS	MS _{den}	<i>F</i> -ratio	<i>p</i>
2014 quadrat surveys						
Crabs	Reserve	1	0.21	0.49	0.43	0.53
	Site [Reserve] & random	5	3.45	0.24	2.89	0.015
	Zone [Site, Reserve]	6	5.69	0.24	3.98	0.0008
	Error	255	53.59			
Shrimp	Reserve	1	0.64	1.32	4.91	0.51
	Site [Reserve] & random	5	9.77	0.49	3.99	0.0017
	Zone [Site, Reserve]	6	4.52	0.49	1.55	0.17
	Error	255	110.13			
2015 crevice surveys						
Crabs	Reserve	1	0.92	0.45	2.06	0.22
	Site [Reserve] & random	4	3.19	0.64	0.69	0.60
	Zone [Site, Reserve]	5	1.78	0.64	0.99	0.43
	Error	122	78.85			
Shrimp	Reserve	1	0.64	10.13	0.06	0.82
	Site [Reserve] & random	4	40.78	0.68	15.01	<0.0001
	Zone [Site, Reserve]	5	2.35	0.68	0.69	0.63
	Error	122	82.84			

different sizes (K-S test, $D = 0.073$ for reserves and $D = 0.76$ for fished areas, with $p = 0.94$ and $p = 0.98$, respectively; Fig. S5 in the Supplement).

Survivorship of tethered shrimp prey was also significantly lower inside reserves (Kaplan-Meier survivability, $\chi^2_{(1)} = 17.42$, $p < 0.0001$; Fig. 3D). After just 1 h, shrimp abundance was reduced to less than half at reserve sites ($55 \pm 4\%$ alive), compared to fished sites ($65 \pm 3\%$ alive). All shrimp were consumed within 48 h regardless of location. On average, time to reach 50% mortality was 4.6 times slower at fished sites and there was a significant negative association between the time to 50% mortality and the density and biomass of macro-invertebrate predators (Table 3, Fig. 3E,F). In addition, there were negative correlations between the time to 50% mortality and predator abundance for all predator functional groups, such that mortality was highest at the sites with higher predator density and biomass (Table 3). Individual survival curves for each site indicate that shrimp at fished sites survived better than at reserve sites, except for Stillwater Cove, which experienced high mortality (Fig. S6 in the Supplement). Shrimp size distributions were statistically similar before and after 50% mortality occurred, indicating shrimp size did not have an effect on survival (K-S test, $D = 0.051$

for reserves and $D = 0.076$ for fished, with $p = 0.10$ and $p = 0.90$, respectively; Fig. S7 in the Supplement).

3.3. Video analysis of predator abundance, visitation, and strike rates

We did not detect significant differences in relative abundance (F_{\max}) of macro-invertebrates, micro-invertebrates, piscivores, and planktivores from the video analysis (Table 4, Fig. 4A), although the trends for all 4 functional groups indicated higher relative abundance during the tethering experiment at reserve sites. We did detect some site effects for micro-invertebrates and planktivores (Table 4), which mirrored the visual surveys, with higher F_{\max} at Hopkins and Pinnacles, respectively. Mean times until the arrival of the first potential predator (T_{inst}) were significantly faster inside reserves, where macro-invertebrates arrived at the array 2 times faster (Table 4). There

were no significant differences in the T_{inst} of micro-invertebrates, piscivores, or planktivores (Table 4, Fig. 4B), but there were some site effects for micro-invertebrates (quicker time to first arrival at Hopkins). When examined at 30 s intervals, macro-invertebrates arrived more rapidly to the array and spent more time overall at tethering assays inside reserve sites than at fished sites (Fig. 4C). Macro-invertebrates at fished sites arrived later and left sooner than they did in reserves. On average, it took single macro-invertebrates twice as long to arrive at fished sites, and almost 3 times as long for multiple macro-invertebrates to arrive at fished sites as compared to reserves (Fig. 4C).

During the tethering assays, there were several observations of predation by divers that helped identify predators (Fig. S8 in the Supplement). Small sculpins (family Cottidae) were observed consuming tethered shrimp within 20 min of deployment. At select sites, red octopus *Octopus rubescens* were seen consuming tethered crabs (Stillwater Cove and Hopkins). Shrimp videos revealed a variety of different predators consuming tethered shrimp, including the macro-invertebrates, such as kelp greenling *Hexagrammos decagrammus*, cabezon *Scorpaenichthys marmoratus*, and black and yellow rockfish

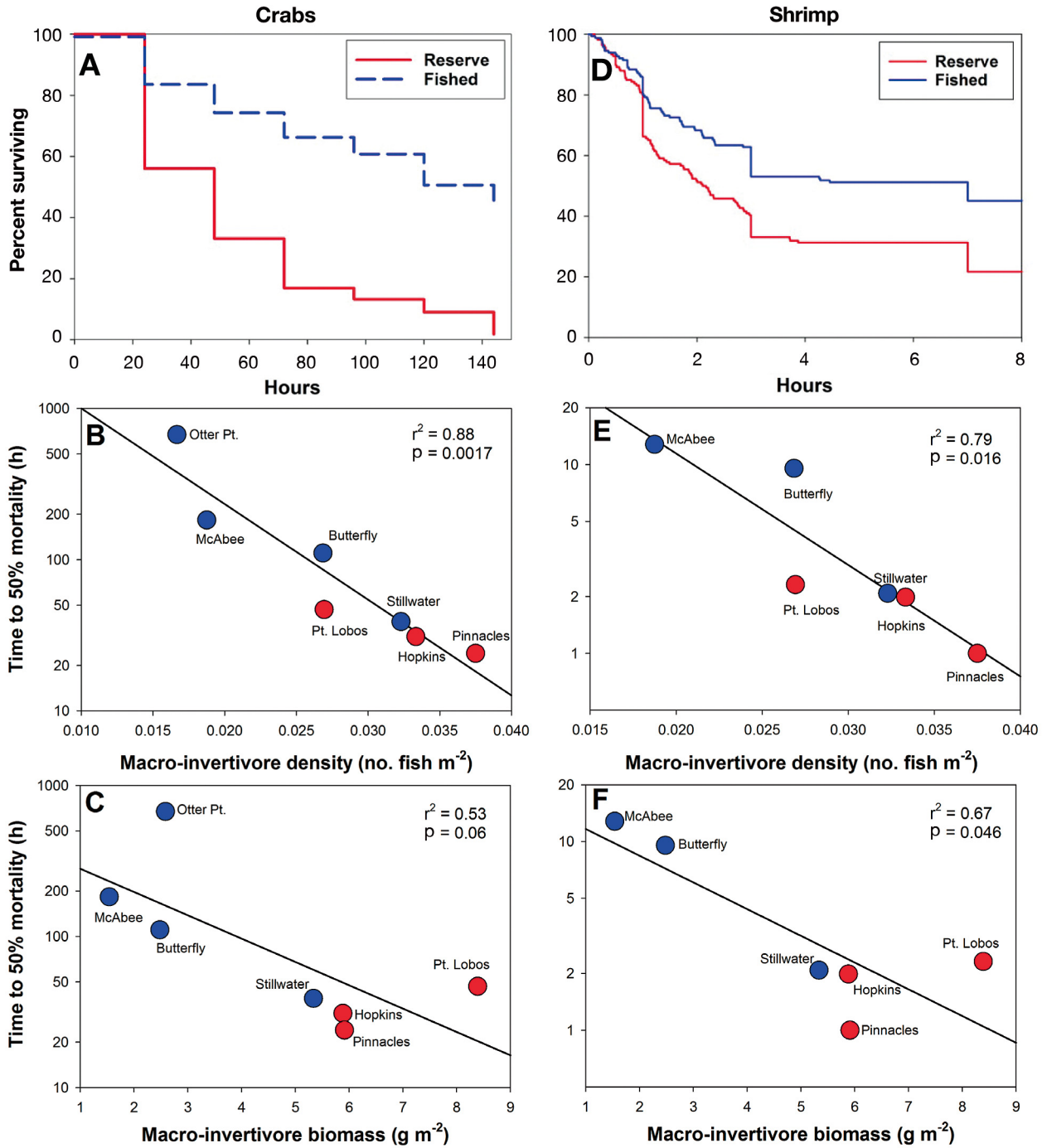


Fig. 3. Crab and shrimp survivorship in tethering experiments by reserve status and relationships between time to 50% mortality and the density and biomass of macro-invertebrate predators for crabs and shrimp. (A) Crab survivorship curves were calculated based on the proportion of prey crabs remaining alive following diver censuses taken at 24 h intervals. See Fig. S4 for site-specific curves. (B,C) Relationship between the time until crabs reached 50% mortality and predator density (B) and biomass (C) in marine reserves (red points) and fished sites (blue points). (D) Shrimp survivorship curves were calculated based on the proportion of prey shrimp remaining alive following diver censuses completed at 0.5, 1, 3, 7, and 24 h intervals and supplemented by real-time underwater video footage. See Fig. S6 for site-specific curves. (E,F) Relationship between the mean time until shrimp reached 50% mortality and predator density (E) and biomass (F) in marine reserves (red points) and fished sites (blue points)

Sebastes chrysomelas, and micro-invertebrates, such as black perch *Embiotoca jacksoni*, striped seaperch *Embiotoca lateralis*, and small sculpins (Cottidae).

In general, more predatory strikes occurred inside reserves than at fished sites across all locations (Fig. 5B), except in the comparison of Pinnacles

Table 3. Correlations between predator abundance and the time to 50% mortality for crabs and shrimp in the experiments. Shown are correlation coefficients (r) and p-values. Significant p-values ($p < 0.05$) are given in **bold**

Factor	Crabs time to 50% mortality		Shrimp time to 50% mortality	
	r	p	r	p
Density				
Macro-invertivore	-0.938	0.0017	-0.894	0.016
Micro-invertivore	-0.555	0.20	-0.549	0.26
Piscivore	-0.655	0.11	-0.712	0.11
Planktivore	-0.496	0.26	-0.515	0.30
Total invert predator	-0.693	0.084	-0.657	0.16
Biomass				
Macro-invertivore	-0.737	0.060	-0.820	0.046
Micro-invertivore	-0.617	0.14	-0.661	0.15
Piscivore	-0.488	0.27	-0.584	0.22
Planktivore	-0.562	0.19	-0.535	0.27
Total invert predator	-0.736	0.055	-0.817	0.047

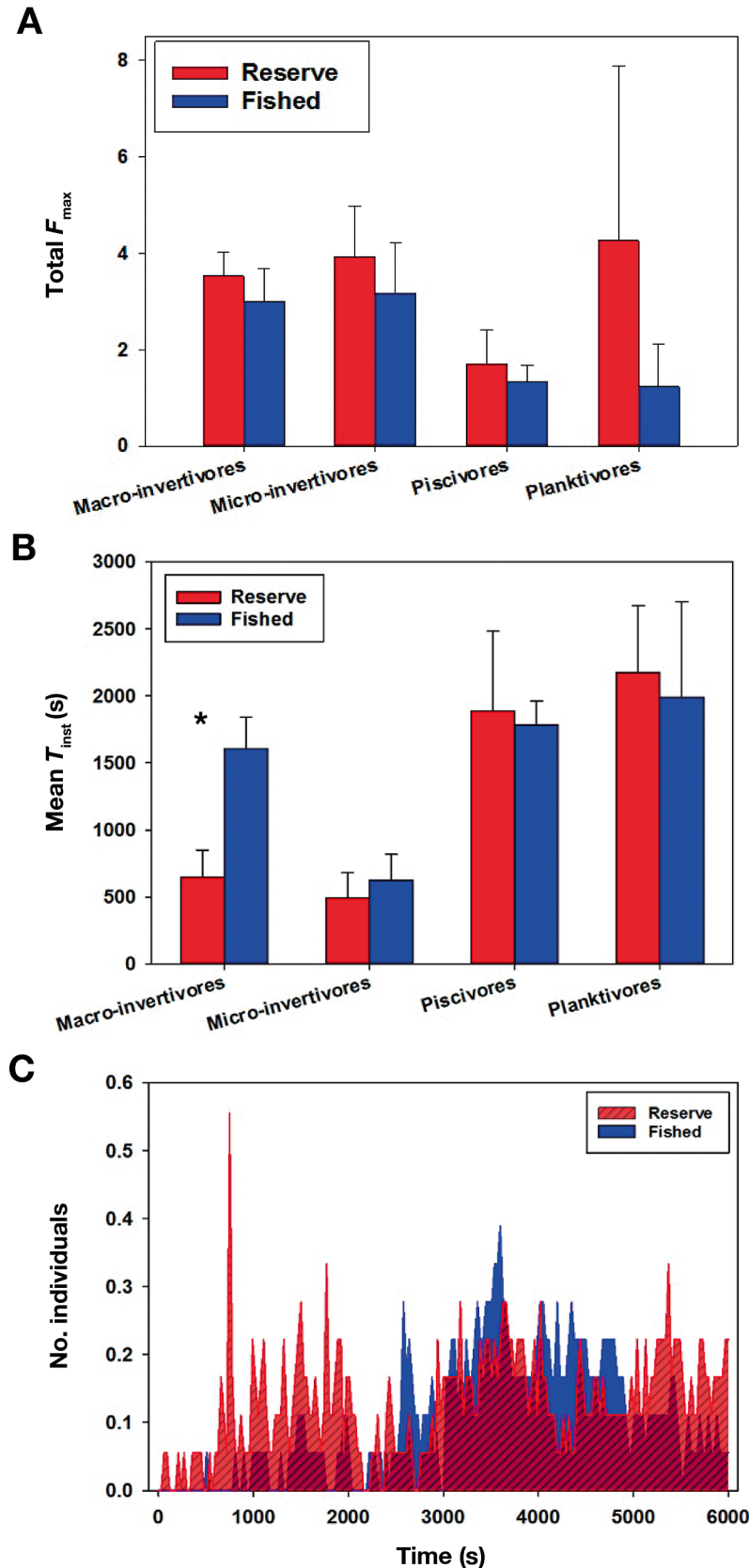
Table 4. Statistical model results testing for differences in F_{max} and T_{inst} of predator functional groups across the study locations. Models include the factors Reserve status and Site (nested within Reserve status). Replicates are individual Go-Pro cameras deployed at each site ($n = 6$) during tethering experiments. MS_{den} : mean square term for the denominator used to calculate the F -ratio. Significant p-values (< 0.05) are given in **bold**

Model	Factor	df	SS	MS_{den}	F -ratio	p
F_{max}						
Macro-invertivore	Reserve	1	2.37	5.65	0.42	0.52
	Site [Reserve]	4	24.20	5.65	1.07	0.38
	Error	29	164.03			
Micro-invertivore	Reserve	1	4.97	4.81	1.03	0.32
	Site [Reserve]	4	76.96	4.81	3.99	0.011
	Error	29	139.53			
Piscivore	Reserve	1	1.17	2.09	0.56	0.46
	Site [Reserve]	4	20.35	2.09	2.43	0.07
	Error	29	82.69			
Planktivore	Reserve	1	80.14	39.81	2.01	0.17
	Site [Reserve]	4	486.97	39.81	3.06	0.032
	Error	29	1154.36			
T_{inst}						
Macro-invertivore	Reserve	1	7433410.0	1061241.0	7.00	0.013
	Site [Reserve]	4	3261867.4	1061241.0	0.76	0.55
	Error	27	28653494			
Micro-invertivore	Reserve	1	145838.2	104494.0	1.40	0.25
	Site [Reserve]	4	2291694.5	104494.0	5.49	0.023
	Error	27	2821328.6			
Piscivore	Reserve	1	61291.9	3097850.0	0.019	0.88
	Site [Reserve]	4	7588164.7	3097850.0	0.62	0.65
	Error	19	58859154.0			
Planktivore	Reserve	1	114330.0	3210081.0	0.034	0.85
	Site [Reserve]	4	14437097.0	3210081.0	1.12	0.39
	Error	13	41731055.0			

(reserve) and Stillwater (fished), resulting in a non-significant effect of Reserve status on the average strike rate observed from video (nested ANOVA: Reserve status, $F_{1,25} = 0.62$, $p = 0.44$; Site[Reserve status], $F_{4,25} = 3.5$, $p = 0.028$).

The ratio of successful to unsuccessful strikes per hour on tethered shrimp was significantly greater for macro-invertivores only (2-sample t -test, $t_{60} = 3.63$, $p = 0.0006$; Fig. 5A). Micro-invertivore species were also successful at striking and consuming tethered shrimp; however their success rate was nearly equal to the unsuccessful rate (Fig. 5A). Fishes from the piscivore and planktivore functional groups rarely made strikes at the shrimp prey; however 7 of 10 strikes made by *Sebastes atrovirens*, a piscivore/omnivore, and only 1 of 2 strikes made by *Sebastes mystinus*, a planktivore/omnivore, were successful. Overall, there were significant differences in the strike rates of the different functional groups (2-way ANOVA, Reserve status, $F_{1,116} = 0.17$, $p = 0.69$; Functional group, $F_{3,116} = 22.17$, $p < 0.0001$; Reserve \times Functional group, $F_{3,116} = 0.14$, $p = 0.94$), with the invertebrate predators (i.e. macro- and micro-invertivores) attacking tethered shrimp at higher rates (Fig. 5A). We also observed spatial variability in which species were actively attacking crustacean prey across sites. An important macro-invertivore, kelp greenling *H. decagrammus*, had an elevated percentage of successful strikes inside reserves (25.5%), while painted greenling *Oxylebius pictus* exhibited a high percentage of unsuccessful strikes inside reserves (43.8%) (Fig. S9 in the Supplement). Among fished sites, kelp greenling had the greatest percent of successful strikes (36.0%), and small sculpins (10 to 14 cm) (*Orthonopias triacis*, *Artedius* spp., *Jordania zonope*) displayed the greatest percentage of unsuccessful strikes (55.4%). Painted greenling and small sculpins had opposite patterns of success inside reserve and fished sites: painted greenlings made proportionally more strikes and were largely unsuccessful in reserves, and sculpins made more strikes and were largely unsuccessful in fished sites (Fig. S9).

4. DISCUSSION



No-take marine reserves in central California significantly influenced predator populations and predatory behavior, including elevated density and biomass of invertebrate predators inside reserves. This translated into significantly higher predation rates on both crabs and shrimp inside reserves, driven by a strong negative association between predator abundance/biomass and the time to 50% mortality for both prey types. In addition, we observed reduced times until the arrival of the first invertebrate predators inside reserves (2 times faster), and elevated strike rates on tethered shrimp inside 2 of the 3 reserves. The invertebrate predators successfully attacked more crabs and shrimp prey than the other functional groups, and within invertebrate predators the macro-invertivores were more successful in every strike attempt than micro-invertivores.

The differences in fish abundance between reserve and fished sites were stronger when quantified by biomass rather than density; fish densities inside reserves were significantly higher for micro-invertivores, whereas biomass inside reserves was significantly higher for macro-invertivores and micro-invertivores, and the effect size was much larger for all functional groups. Because biomass is a product of density and size, the biomass results indicate that the invertebrate predators were also larger inside reserves.

Fig. 4. (A) Fish abundance (F_{max}) from video observations by reserve status. Means (± 1 SE) were calculated from sums of each unique predator (F_{max}) observed within a half-meter of the tethering assay at one time. (B) Mean time (± 1 SE) until the first arrival (T_{inst}) of predatory fishes in marine reserves and fished sites for each functional group. *Significant difference in times between reserve and fished sites ($p < 0.05$). (C) Arrival times and variability in the abundance of macro-invertebrate predatory fishes by reserve status. Mean abundance was calculated every 30 s for the first 6000 s of video footage

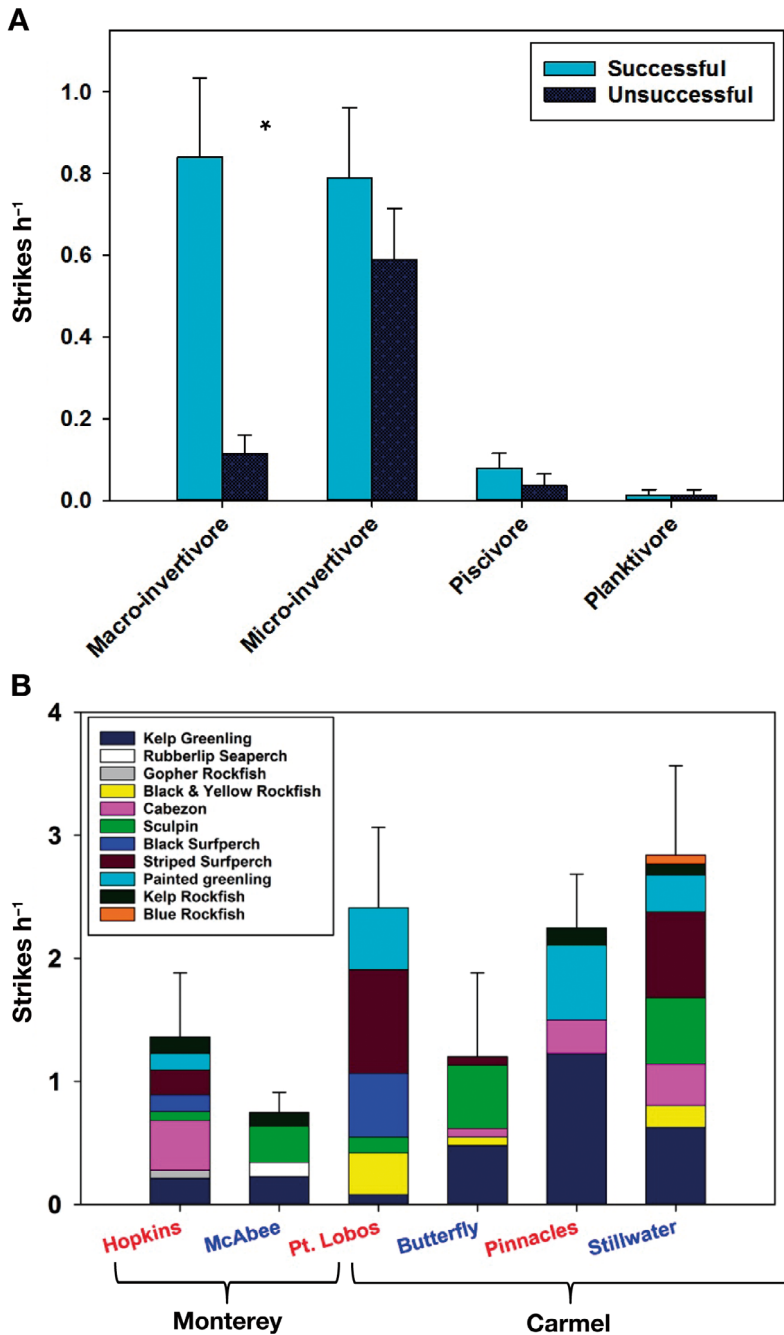


Fig. 5. (A) Mean number of strikes per hour that were successful or unsuccessful by fish functional groups. (B) Number of strikes per hour for different predator species by site. Red text indicates reserve sites and blue indicates fished sites. For both plots, means (± 1 SE) were calculated from the number of observed attacks per hour during shrimp tethering experiments. *Significant difference between successful and unsuccessful strike attempts ($p < 0.05$)

Numerous studies have demonstrated that predator body size is often positively correlated with consumptive effects (e.g. Hamilton & Caselle 2015, Selden et al. 2017), and thus the combination of larger predators and more numerous predators likely

magnified prey mortality in our tethering experiments. Our results indicated that fish biomass of invertebrate predators was almost 3 times greater inside reserves than outside on the central California coast. Previous studies in central California reported fish biomass to be 2 times greater inside reserves (Paddock & Estes 2000), while studies in southern California found biomass of fishes targeted by anglers to be 4 times greater inside reserves (Caselle et al. 2015). The non-significant differences in density of most predator functional groups between reserve and fished sites could be explained by variability in recruitment and slow growth characteristic of species living within the California current ecosystem, which lengthens the time for some species to respond to reserve protection (Kaplan et al. 2019), and the relatively light fishing pressure that occurs in some areas of the central California coast. Starr et al. (2015) indicated that reserves in central California may require 20 or more years to exhibit significant recovery of some fish species. These results have been verified by modeling studies which indicate that reserve responses of central California species depend on MPA age, fishing pressure outside the reserve, and the life history characteristics of targeted species (Kaplan et al. 2019, Nickols et al. 2019). The present study found much stronger responses of reserves on metrics of biomass than density, which aligns with other field (Hamilton et al. 2010, Caselle et al. 2015) and modeling (Kaplan et al. 2019) studies indicating that biomass often responds more rapidly than abundance to reserve protection. Biomass of organisms inside reserves in temperate and tropical reserves worldwide averages 4 to 5 times higher than comparable fished areas, while densities

are only 2 to 3 times higher (Lester et al. 2009).

We did not detect significant differences in the abundance of crustacean prey species between reserve and fished sites. However, the 2 different survey methods (random quadrats vs. targeted crevice

surveys) employed in different years showed similar patterns of prey abundance: higher crab and lower shrimp densities inside reserves, and higher shrimp densities at the Monterey vs. Carmel sites. We also did not detect any significant associations between predator abundance and prey abundance, although for most comparisons there was a trend for invertebrate prey to be less abundant at the sites with the most predators. A study in temperate waters off Australia estimated that red bait crabs *Plagusia chabrus* were slightly (1.5 times) more abundant inside protected areas than outside, but the pattern was obscured by high variability and small sample size (Pederson & Johnson 2006). Although crustacean populations did not vary between reserve and fished sites, it has been suggested that indirect effects mediated by reserve protection may take decades to occur (Babcock et al. 2010). In this instance, having similar prey densities was useful because it ensured that predation rates at the tethering assays were not affected by systematic differences in background prey availability.

Mortality of crabs and shrimp at tethering assays was significantly higher inside reserves and this pattern is consistent with similar studies globally. Our results demonstrate that predation on decapod crustaceans was 4.6 to 7 times greater inside reserves, where predatory fishes were more abundant. A recent study, also in Monterey and Carmel Bays, indicated predation rates by macro-invertivores and piscivores on tethered squid prey were 6.5 times higher, and per capita feeding rates were 1.9 times higher inside older reserves (Point Lobos and Hopkins) compared to newly protected areas (Rhoades et al. 2019). In contrast, we found similar predator–prey responses in the older reserves (Point Lobos and Hopkins) compared to the new reserve (Pinnacles), likely because predators were very abundant at the new reserve (which may be attributed to the offshore location of the Pinnacles site). In coastal temperate waters in the Gulf of Maine, predation on tethered brittle stars was 4 to 10 times higher and predation on rock crabs was 21 times greater at offshore, non-fished sites than in coastal, historically overfished sites (Witman & Sebens 1992). In southern California, Selden et al. (2017) demonstrated that higher biomass of fish predators translated into elevated mortality rates of urchins inside reserves compared to fished areas. Predator size was a significant predictor of consumptive effects and larger predators consumed more urchins and larger urchins inside reserves. Tethering studies indicate higher mortality inside reserves in subtropical regions for urchins (e.g. Sala & Zabala

1996, Shears & Babcock 2002, Guidetti 2006) and juvenile lobsters (Loflen & Hovel 2010), and in tropical regions for urchins (McClanahan & Muthiga 1989) and shrimp (Ory et al. 2014). Collectively, these results provide strong evidence that an increase in predatory fish abundance inside reserves translates to the increased mortality of various species of benthic invertebrate prey species (i.e. urchins, gastropods, brittle stars, crabs and shrimp).

Species of fishes observed striking tethered shrimp during predation assays were natural predators of shrimp, including *Hexagrammos decagrammus*, *Scorpaenichthys marmoratus*, *Embiotoca lateralis*, *Oxyplebius pictus*, and small sculpins (family Cottidae). Diet studies of central California kelp forest fishes characterize most demersal fishes as trophic generalists (Love 2011), with some focusing more on invertebrates, and some on fishes. *H. decagrammus* typically feed on crustaceans, polychaete worms, brittle stars, mollusks, and small fishes (Armstrong 1996); *S. marmoratus* typically feed on crustaceans, fishes and mollusks (Hart 1973); *E. lateralis* feed on crustaceans, worms, and mussels, and occasionally herring eggs (Clemens & Wilby 1961); and *O. pictus* feed on crustaceans, polychaetes, small mollusks, and small bryozoans (Fitch & Lavenberg 1975). Therefore, crustaceans comprise a major component of the diet of all the predatory fishes observed feeding on shrimp at tethering assays. These predators, however, did vary in the number of successful feeding strikes during predation assays. Macro-invertivores made a significantly larger proportion of successful to unsuccessful strikes on shrimp compared to micro-invertivores, planktivores, and piscivores. As expected due to gape size, larger invertebrate predators are more successful than smaller species when presented shrimp of various lengths (15 to 80 mm). This is also a reasonable outcome since predator length is often proportional to prey length (Scharf et al. 2000).

Abundances of invertebrate predators, F_{\max} , did not differ between reserve and fished sites as quantified from video footage; however, the trends were similar to visual fish surveys, with more predators from each functional group observed inside reserves. As mentioned previously, biomass is likely a much more important metric for considering predator consumptive effects than abundance alone. Numerous studies have determined that it is more effective to utilize multiple methods of survey techniques when quantifying fish abundances in order to account for variation in body size, habitat partitioning, aggregation behavior, and behavioral responses to divers (Willis & Babcock 2000). The GoPro video footage

collected from tethered assays was analyzed as a remotely operated survey technique, similar to existing baited remote underwater video (BRUV) techniques, in order to supplement diver surveys. The abundance metric extracted from the video (F_{\max} ; maximum number of individuals of a species observed in a single frame) is also highly conservative and may underestimate abundance in trying to avoid double counting individuals. We did find that macro-invertebrates arrived at tethered assays (T_{inst}) inside reserves in half the time it took them to arrive at assays at fished sites, which may help to explain the high consumption of prey inside reserves. Rockfishes inside many of these same reserves in central California are bolder and less risk averse in the presence of divers (Rhoades et al. 2018) and may have been more willing to inspect and attack prey at the tethering arrays deployed at the reserve sites. Similar decreases in T_{inst} of predators have been observed using BRUVs inside reserves in New Zealand (Willis & Babcock 2000).

The results from this study indicate that predator recovery inside marine reserves has the potential to affect prey populations following the cessation of fishing pressure, due to an increase in predation pressure. These indirect effects of marine reserves on prey mortality have been reported from New Zealand, Australia, California, Kenya, and the Philippines, and often take over a decade to occur (Babcock et al. 2010). Most of the macro- and micro-invertebrates in this study, especially rockfishes, are generalist secondary carnivores that consume a wide diversity of prey items (Love 2011). While crab and shrimp populations currently occur at similar densities in reserve and fished sites, it is unknown if they started off this way at the time of reserve establishment. Alternatively, it may require more time for the effects of predators to significantly alter prey numbers. In addition, trophic interactions may have additional complex indirect effects in central California kelp forests. For example, lingcod are a fished species and the most voracious piscivore in the system. Studies have shown that predation by lingcod on rockfishes is 3 times greater inside reserves versus outside (Beaudreau & Essington 2007). In Vancouver, British Columbia, there is evidence that this may result in a cascade of effects in which an abundance of lingcod inside reserves limits the abundances of lower carnivores (e.g. rockfishes), and in turn the magnitude of predation by rockfishes on their invertebrate prey (e.g. shrimp; Frid & Marliave 2010). It is likely that the reestablishment of larger fishes inside reserves in central California may have

similar cascading effects that are manifest throughout the food web in complex and context-specific ways.

5. CONCLUSIONS

Predatory fishes play an important role in ecosystems via consumptive and non-consumptive effects, it is imperative to utilize existing areas of spatial variation in predator abundance as a means to understand these effects. In ocean ecosystems, the varying predator densities created by marine reserves and adjacent fished zones currently serve as an effective method to study impacts of predatory fishes while controlling for habitat variation or other factors. In temperate zones such as central California, networks of marine reserves provide an ideal framework for such experiments. In order to determine the ultimate role of predatory fishes in central California kelp forest communities, one must first determine the relationship between fish densities and fish predation rates in these areas. The present findings demonstrated a 4- to 7-fold increase of predation upon 2 species of invertebrates inside marine reserves. Empirical studies like this are instrumental in uncovering the ecological consequences of human impacts on the oceans, and developing methods to mitigate those effects.

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