

ARTICLE

Special Feature: Honoring Charles H. Peterson, Ecologist

Increasing spillover enhances southern California spiny lobster catch along marine reserve borders

Hunter S. Lenihan¹ | Sean P. Fitzgerald^{1,2} | Daniel C. Reed³ |
 Jennifer K. K. Hofmeister⁴ | Adrian C. Stier^{3,5} 

¹Bren School of Environmental Science and Management, University of California, Santa Barbara, California, USA

²Florida Fish and Wildlife Conservation Commission, Tallahassee, Florida, USA

³Marine Science Institute, University of California, Santa Barbara, California, USA

⁴California Department of Fish and Wildlife, San Diego, California, USA

⁵Department of Ecology, Evolution and Marine Biology, University of California, Santa Barbara, California, USA

Correspondence

Hunter S. Lenihan
 Email: hlenihan@ucsb.edu

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Abstract

The conservation benefits of marine reserves are well established but their contribution to adjacent fisheries via spillover is less certain and context-dependent. Theoretical predictions do not always match empirical evidence from individual reserves, so carefully designed studies are essential for accurately assessing spillover and its contribution to fisheries. Biomass buildup within reserves, and spillover from reserve borders, also usually takes time to develop. In 2003, a network of no-take marine reserves was established in the Northern Channel Islands (NCI) of southern California (CA) to conserve biodiversity and to eventually enhance local fisheries through spillover of larvae, juveniles, and adults. The reserve network impacted the local CA spiny lobster (*Panulirus interruptus*) fishery by removing about 20% of fishing grounds in the NCI. In 2008, a collaborative fisheries research effort detected substantial lobster population increases within reserves, and an indication of the possible spillover of adult lobsters across reserve borders. To estimate whether and how much populations within reserves, and spillover from reserves, have increased through time, we repeated the sampling program 10 years later in 2018 at two of the three original reserves. Scientific trapping was conducted prior to the fishing season along a spatial gradient beginning deep within the reserves to reference sites located outside (≥ 2 km) of reserve borders. Results showed that legal-sized lobster abundance in traps (catch per unit effort) increased by 125%–465% deep inside reserves, and by 223%–331% at sites near to reserve borders, and by nearly 400% just outside of reserve borders over the 10-year period, thus indicating a substantial increase in spillover across reserve borders. A similar pattern was observed in lobster biomass caught in traps at the two reserves. This study demonstrates how spillover scales with biomass buildup and that collaborative fisheries research can be used to assess the efficacy of marine reserves as fishery management tools worldwide.

KEY WORDS

collaborative fisheries research, fishery benefits, marine reserves, *Panulirus interruptus*, Special Feature: Honoring Charles H. Peterson Ecologist, spillover, spiny lobster

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INTRODUCTION

Marine reserves are no-take marine protected areas (MPAs) that are widely recognized as effective conservation tools for protecting marine resources within their borders (Byers, 2005; Di Franco et al., 2016; Lubchenco et al., 2003; Sala & Giakoumi, 2017). Establishing and enforcing marine reserves often lead to the increased size, density, and spawning biomass of harvested species. Theory predicts that marine reserves can increase the reliability of exploitable fish stocks for the benefit of fishers (Lester et al., 2009; Roberts et al., 2005; Russ & Alcala, 2011). One mechanism by which reserves can benefit fisheries is through “spillover,” of which there are two main forms. First, protection from fishing can lead to an increase in the abundance and biomass of reproductive adults that produce relatively many eggs or larvae that disperse from within reserve borders to areas outside of reserves, where animals can be harvested (e.g., Botsford et al., 2009; Gell & Roberts, 2003; Pelc et al., 2010). Jennings (2000) described this mechanism as increases in spawner biomass per recruit and larval supply by protecting “source” populations. Second, an increase in the population density, and individual size of animals within a reserve, can stimulate juvenile and adult individuals to migrate from inside to outside of reserve borders in search of food, habitat, or mates, or to avoid aggressive interactions with conspecifics (e.g., Di Lorenzo et al., 2016, 2020; Halpern et al., 2010; Kellner et al., 2007). Both mechanisms of spillover can enhance fisheries by increasing the overall biomass of target species available for harvest in open fishing grounds. However, the capacity for marine reserves to benefit adjacent fisheries through spillover is controversial and an active area of research (Hilborn et al., 2004; Parrish, 1999; Woodcock et al., 2017). This controversy arises, in part, from the clear short-term costs to fishers associated with reserve implementation, which typically includes the reduction in the size of available fishing grounds (Di Lorenzo et al., 2016; McClanahan, 1999). In addition, the spillover of juveniles and adults is thought to enhance only fisheries in which intensive fishing has substantially depleted the stock to such a degree that the addition of individuals through spillover has a detectable positive effect on catch (Halpern et al., 2010; Walters et al., 2007; but see Lenihan et al., 2021).

While theory and some empirical evidence suggest that reserves can benefit adjacent fisheries through spillover, despite the closure of fishable habitat (Follesa et al., 2011; Goñi et al., 2010; Kerwath et al., 2013; Lenihan et al., 2021), other studies have failed to identify clear evidence of spillover benefits (Willis et al., 2003). Evaluation of what underlies the long-term benefits of

marine reserves as fishery management tools requires ongoing site-specific empirical study (Caselle et al., 2015; De Leo & Micheli, 2015; Kay, Lenihan, Guenther, et al., 2012; Sale et al., 2005). Whether and to what extent reserves provide net economic benefits to a fishery through spillover depends on a suite of biological, social, and economic factors that usually take time to develop (Lynham et al., 2020). Even after protection occurs and mortality from harvest goes down inside reserves, it usually takes time for most species to build up in biomass inside a protected area (Kaplan et al., 2019). Additionally, when reserves restrict access to certain fishing grounds, it may take time for fishers to adapt and find new places to fish (Guenther et al., 2015).

One way to better understand the fisheries consequences of reserve implementation is to examine how reserves affect both the harvested species and catch through time (Lenihan et al., 2021). Specifically, we can quantify temporal changes in the biomass, size structure, and density of harvested species inside of reserves, and then relate the patterns we observe to the catch per unit effort of the harvested species (CPUE) measured outside of reserves (Goñi et al., 2011). Here, we use multiple estimates of catch per unit effort and biomass to examine the response of CA spiny lobster (*Panulirus interruptus*) populations to reserve protection in southern CA, and to test whether increases in lobster abundance and size inside reserves have led to greater catch through spillover in nearby fishing grounds.

Lobster species have been the focus of relatively many studies designed to assess the ecological performance of marine reserves (Babcock et al., 1999; Bevacqua et al., 2010; Edgar & Barrett, 1999; Goñi et al., 2006; Shears et al., 2006) and the effects of reserves on fisheries (e.g., Follesa et al., 2011; Goñi et al., 2010, 2011; Ley-Cooper et al., 2014; Moland et al., 2013). Lobsters are relatively long-lived (30–100 years) and highly fecund (millions of eggs) marine benthic predators whose larvae can spend long periods of time (6–12 months) in a planktotrophic dispersive state. Much attention has been paid to lobsters because many species are relatively very heavily fished due to their high value, and many of their biological characteristics, especially a benthic life history as juveniles and adults, and a relatively limited range of movement (~1–2 km) as adults, mean that even relatively small reserves are effective tools for conservation (Kramer & Chapman, 1999; Le Quesne & Codling, 2008; Moffitt et al., 2009; Moland et al., 2011). Nevertheless, the results of studies designed to quantify the spillover of relatively many lobster species have varied widely. Some studies detected spillover and associated fishery benefits (Bevacqua et al., 2010; Follesa et al., 2011; Goñi et al., 2006, 2010; Kerwath et al., 2013; Lenihan

et al., 2021; Ley-Cooper et al., 2014; Moland et al., 2013), while others found no evidence of the spillover of legalized individuals (Hoskin et al., 2011; Rowe, 2002) or found spillover only for relatively very larger lobsters (Thorbjørnsen et al., 2018). Additionally, for Caribbean spiny lobsters in Florida, one study found that lobsters “spill in” to reserves in response to disturbance (Eggleson & Parsons, 2008).

Variation in the presence/absence, intensity, and dynamics of lobster spillover reported in marine reserve literature may reflect several key factors, including a wide array of different lobster species and environmental settings. Poaching within reserves is an ubiquitous and often unaccounted for problem (Byers & Noonburg, 2007). Lobsters also may not consistently migrate over reserve boundaries, or if they do, the amount of net migration out of reserves may not be enough to influence local catch rates. Such a scenario is possible when lobster abundance and catch were relatively high before reserves were implemented (Halpern et al., 2009; Hilborn et al., 2004). Additionally, the fishery may not actively fish reserve borders if there is not suitable habitat along reserve borders (Freeman et al., 2009; Guenther et al., 2015; White et al., 2020). The response of recovering species inside reserves can also be long and transient (White et al., 2013). Thus, it may take substantial time for populations to increase sufficiently enough inside reserves to cause the net movement of animals from inside to outside of reserves where they are harvested (Hilborn et al., 2006; Jiao et al., 2018).

The implementation of a marine reserve network in the Northern Channel Islands (NCI), California (CA), USA, in 2003 had major impacts on the southern CA spiny lobster fishery. Prior to the establishment of the reserve network, lobster populations were heavily exploited (California Department of Fish and Game [CDFG], 2008), but the fishery was considered sustainable by fishers and managers (Neilson, 2011). The placement of reserves and the total amount of area protected from fishing effectively removed ~17% of lobster fishing grounds in the NCI (Guenther et al., 2015). Whether reserve establishment influenced the total catch of lobsters in the region has not been tested, but interviews with 65% of fishers within the NCI lobster fleet indicated that individual catch rates had declined by an average of 10% during the six periods (2003–2008) after reserves were established (Guenther, 2010). To clarify, reserves were established prior to the lobster fishing season (October–March) in 2003. Research on the effects of NCI reserves on spiny lobsters showed that by 2008, there were substantial increases in lobster abundance and biomass inside reserves (Kay, Lenihan, Guenther, et al., 2012). Spatially intensive research trapping of

adults and juveniles, and tag-and-recovery studies, conducted in collaboration with the local lobster fishery revealed evidence of spillover, albeit in a relatively small amount (Kay, Lenihan, Kotchen, & Miller, 2012). By contrast, results from a before–after–control–impact analysis in the NCI indicated that fishing effort and CPUE for lobster decreased near reserve borders 5 years after reserve implementation due mainly to the fishers choosing not fish near to the reserve borders (Guenther et al., 2015). Thus, the benefits of the NCI reserves to the fishery have remained uncertain (Kay, Lenihan, Kotchen, & Miller, 2012; Withy-Allen & Hovel, 2013).

Anecdotal evidence suggests that, over the past decade, fishers are spending an increasing amount of time fishing the line (i.e., the line that marks the border of MPAs) in southern CA (e.g., Lenihan et al., 2021) and that spiny lobster catch rates and lobster sizes near reserve borders have markedly increased (S. Fitzgerald & H. Lenihan, personal observations). This anecdotal evidence motivated us to examine whether lobster population abundance and spillover detected in 2008 by Kay, Lenihan, Kotchen, and Miller (2012) have increased through time. To do this, we partnered with the fishery to replicate Kay et al.’s study using scientific trapping at two Channel Island MPAs prior to the opening of the fishing season in 2018. Our objectives were to test whether and how much lobster abundance and biomass have increased within the NCI reserves after 15 years of protection from fishing, and whether fishers are experiencing increased catch outside of reserve borders due to spillover. We know of no other study that tested for increases in reserve spillover through time by repeating a spatially explicit experimental fishing regime. We dedicate this research in honor of Charles H. “Pete” Peterson and to his extraordinary body of research that contributed greatly to coastal marine resource management and ecological science.

METHODS

Study sites and data collection

To test how continued, well-enforced protection from fishing influenced lobster populations and catch, we collected size and CPUE data for CA spiny lobster using modified commercial lobster traps placed along a spatial gradient extending from deep within to relatively far outside the borders of two no-take MPAs, Scorpion Marine Reserve and Gull Marine Reserve, located on Santa Cruz Island in the Santa Barbara Channel (SBC) (Figure 1). A total of 13 marine reserves were established in the SBC in April 2003 (CDFG, 2008). A full description of the

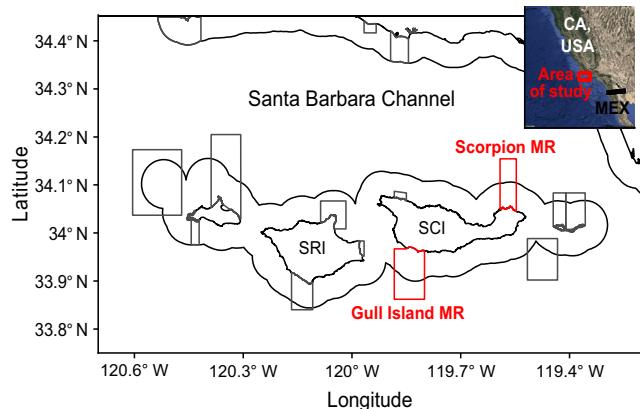


FIGURE 1 Map showing the study area in the southern California Bight, including the Santa Barbara Channel and the Northern Channel Islands. Black lines indicate the coast and the state boundary three nautical miles offshore. The two largest islands are labeled (SCI, Santa Cruz Island; SRI, Santa Rosa Island). Rectangles (dark gray) represent marine reserves (MR); the reserves sampled in this study (Scorpion and Gull Island) are highlighted in red. MEX, Mexico.

physical, ecological, and oceanographic characteristics of the Scorpion and Gull reserves and sampling sites is provided in Kay, Lenihan, Guenther, et al. (2012) and Kay, Lenihan, Kotchen, and Miller (2012). In brief, trapping sites were selected based on extensive habitat surveys by divers and local ecological knowledge (LEK) of commercial fishers. Surveys and LEK ensured that sites were appropriate for lobster sampling based on habitat, historical lobster yield, and population size structure, depth, and oceanographic conditions. Each trap was placed in 2018 on the same localized reef patch, but ~30 m away from the initial spot used in 2008, in an effort to promote sample independence. Four trap location categories relative to MPA borders were designated for each reserve: deep inside (“in-deep”), near the inner reserve border (“in-edge”), near the outer reserve border (“out-edge”), and far outside (“out-far”; Figure 2). A prior study found that the use of baited traps to estimate spiny lobster abundance was sufficiently accurate: Estimates from traps were statistically indistinguishable from estimates made by diver counts (Kay, Lenihan, Guenther, et al., 2012).

Trap location designations (in-deep, in-edge, out-edge, and out-far) were based on trap distance from MPA borders as measured by GPS coordinates, fisher LEK of areas with contiguous habitat, and the spatial scale of lobster movement. Tagging studies over a 2-year period (2007–2008) at the Channel Islands showed that most lobsters tagged at the Channel Islands moved ≤ 1 km from their initial tagging site and lobsters rarely moved ≥ 2 km from their initial tagging site (CDFG, 2008; Kay &

Wilson, 2012). As such, we defined out-far sites as ≥ 2 km outside of a reserve border and out-edge sites as ≤ 1 km outside of a reserve border for both MPAs. Inner site designations differed slightly between studies. At Gull Island Reserve (Gull), in-deep traps were those set ≥ 2 km inside the western reserve border (where the remainder of trap sampling took place; see Figure 2). In-edge traps were set ≤ 1 km inside the western border of Gull. At Scorpion Point Reserve (Scorpion), there is a sandy area located $\sim 0.65\text{--}0.85$ km inside the reserve that disrupts the continuous rocky reef habitat. As such, in-deep traps were set ≥ 0.85 km inside the reserve border and in-edge traps were set ≤ 0.65 km inside the reserve border. Fisher LEK supported these designations while at sea. Figure 2 shows the coordinates and categorizations for each trap. Traps with erroneous GPS recordings (i.e., GPS appeared outside of known sampling locations or GPS did not match at-sea trap location designation) and traps that did not closely overlap (>50 m) between the two studies were removed from both datasets. Data from 40 to 122 traps were used from each sampling location in 2018.

Traps were set under the guidance of a commercial fisherman in August and September of 2018, just prior to the opening of the commercial and recreational lobster fishery. Data from the 2008 study were restricted to traps set in August and September as well. Traps were identical to those used in the commercial lobster fishery, with the exception that escape ports for sublegal lobsters were closed to obtain a better representation of population size structure. In addition, differences in the spatial patterns in the CPUE of adult and sublegal juveniles provide an additional test of spillover as sublegals are caught and retained at much lower rates than adults (see Kay, Lenihan, Kotchen, & Miller, 2012). Complete details regarding commercial trap construction and deployment are described in Kay, Lenihan, Guenther, et al. (2012). In brief, traps were deployed haphazardly at 6- to 16-m water depth within areas stratified by reef boundaries (i.e., the extent of hard-bottom substrate) that were delineated prior to sampling based on qualitative scuba surveys, local ecological knowledge (LEK) of collaborative fishery partners, and the distribution of giant kelp (*Macrocystis pyrifera*). As such, the exact position of each trap on the seafloor was not controlled, and replicate traps were separated by ~ 30 m to avoid nonindependence of sampling units. The distance of 30 m was identified a prior by fishery partners as a distance that would not cause traps to compete against each other, and individual lobsters often set their own traps much closer together (see Kay, Lenihan, Guenther, et al., 2012).

For every trap deployed, we recorded depth, GPS coordinates, date, soak time (number of nights a trap was left in the water), number of lobsters caught, and trap

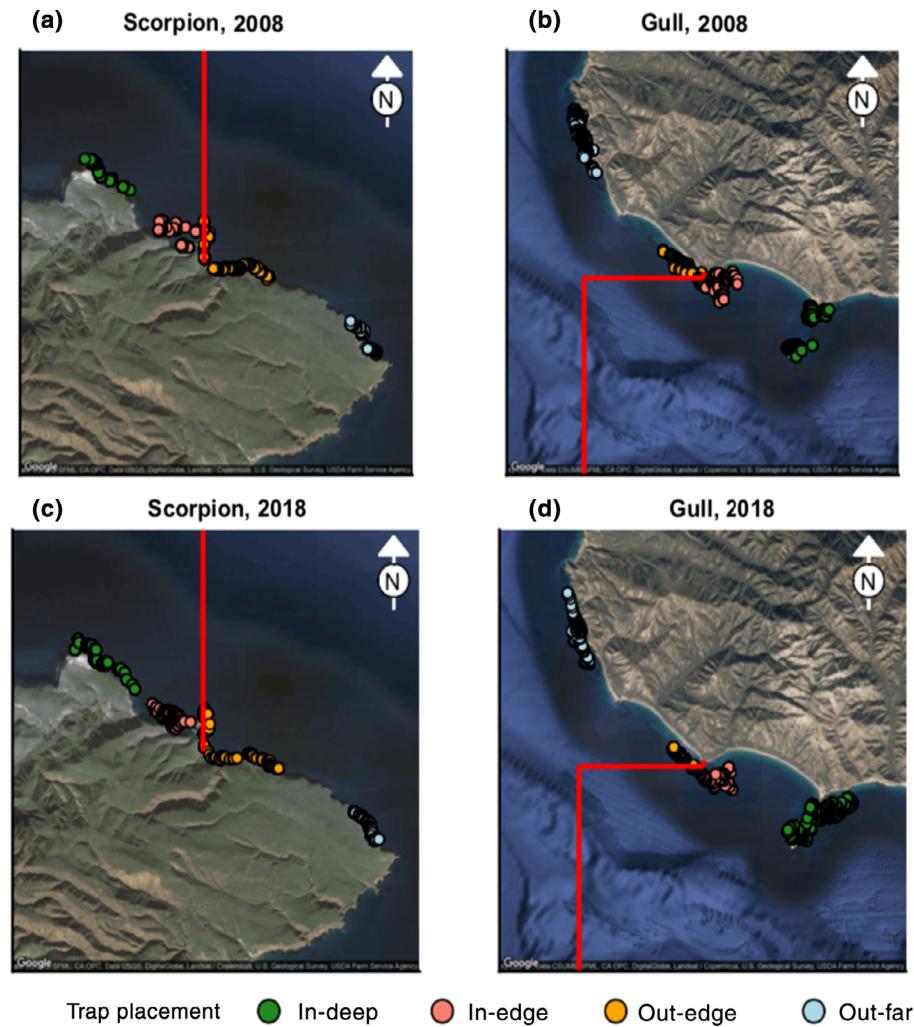


FIGURE 2 Map showing location of each trap pulled relative to border (red) for (a) Scorpion Marine Reserve in 2008 (top left), (b) Gull Island Marine Reserve in 2008 (top right), (c) Scorpion Marine Reserve in 2018 (bottom left), and (d) Gull Island Marine Reserve in 2018 (bottom right). Circle colors represent trap location designation (green, in-deep; salmon, in-edge; orange, out-edge; and light blue, out-far). Scorpion, Scorpion Marine Reserve; Gull, Gull Island Marine Reserve.

location designation. We also recorded the sex of every lobster caught in every trap, and measured and recorded every lobster's carapace length (CL; in millimeters) to the nearest two decimal points using Mitutoyo 500-763-10 IP67 Absolute Coolant Proof Calipers. While docked inside Scorpion, we also measured lobster weight to the nearest 0.01 kg using a Gempler's digital hanging scale (model number 227658) for a subset of lobsters ($n = 114$) that covered the size spectrum for both sexes sampled in this study. All lobsters were kept in the shade to reduce stress and were released in their original location.

Standardizing data for soak time

An important difference between the 2008 and 2018 studies was the number of nights a trap was left in the water

(soak time). All other methodology used in 2018 was the exact same as that used in 2008. Our own at-sea observations, fisher LEK, and results from Kay, Lenihan, Kotchen, and Miller (2012) show that soak time significantly affects trap CPUE at the Channel Islands, and traps soaked for fewer nights in this study (1.9 ± 0.8 nights, mean \pm SD) compared with 2008 (4.5 ± 1.6 nights; Welch's $t_{1729.6} = 47.202$, $p < 0.0001$). As such, data required standardization to account for soak time. Modeling efforts suggested that the nature of the relationship (i.e., linear or nonlinear) between soak time and catch per trap varied depending on the number of nights soaked, perhaps due to trap saturation occurring after multiple nights. The significance and magnitude of soak time's influence on catch per trap were also specific to different combinations of trap location and year (Appendix S1: Tables S1 and S2 provide model details

and further explanation). We therefore assessed the effect of soak time separately for each combination of year (2008 or 2018), MPA (Gull or Scorpion), and trap location (in-deep, in-edge, out-edge, and out-far) using the equations:

$$\text{Catch per trap (in kilograms or number of lobsters)} = \beta_0 + \beta_1 \text{Soak} + \epsilon \quad (1)$$

and

$$\text{Catch per trap (in kilograms or number of lobsters)} = \beta_0 + \beta_1 \text{Soak} + \beta_2 (\text{Soak})^2 + \epsilon, \quad (2)$$

where β_0 is the intercept, Soak is a continuous variable representing the number of nights a trap was left in the water, the $(\text{Soak})^2$ term in Equation 2 allows for a nonlinear relationship between soak time and catch per trap, β_1 and β_2 are the regression coefficients on Soak and $(\text{Soak})^2$, respectively, and ϵ is an error term describing variance not explained by the regression.

When a model demonstrated a significant relationship between soak time and catch per trap for a given year–MPA–location combination, the best-performing model (Equation 1 or 2) was selected based on Akaike information criterion (AIC) and R^2 values. Raw data entries were then standardized to represent the average value for a 3-night soak (the median soak time across all data) by multiplying each data entry by the ratio $3_{\text{night}}/i_{\text{night}}$, where 3_{night} is the model-predicted value for a 3-night soak, and i_{night} is the model-predicted value for the actual number of nights soaked for the given trap (1–8 nights).

When catch per trap was not significantly affected by soak time (i.e., $p > 0.05$ for β_1 in Equation 1, $p > 0.05$ for β_1 or β_2 in Equation 2), raw data were not standardized. Linear and nonlinear model results assessing soak time for each year–MPA–location combination are in Appendix S1: Tables S3–S10. In rare cases where model diagnostics suggested similar fits for linear and nonlinear models, the more conservative data transformation was applied (i.e., data were adjusted to a lesser degree). The catch per unit effort of the harvested species (numbers) and weight per trap data (in kilograms) were standardized for 7 of 16 year–MPA–location combinations, which changed mean catch per trap values by 15%–48% (Appendix S1: Tables S11 and S12).

Data analysis

We assessed changes in catch per trap from 2008 to 2018 in terms of CPUE (numbers per trap) and weight per trap

(in kilograms) of legally sized lobsters using two-sample hypothesis testing for each combination of MPA and trap location (e.g., Gull in-deep CPUE in 2008 = Gull in-deep CPUE in 2018). Data for most year–MPA–location combinations exhibited non-normality, skewness, and unequal variances between sites and years regardless of log or square root transformation, so we used Welch's t test approximation to compare groups and used untransformed data to provide the simplest possible interpretation of test results. Welch's test is more reliable than other two-sample hypothesis testing methods when variances are unequal (i.e., Student's t test, Mann-Whitney U ; Ruxton, 2006; Zimmerman et al., 1993), and was the most robust method when comparing samples similar to ours in terms of unequal levels of skewness, variance, and sample size (the true significance level was within 10%–20% of the nominal significance value; Fagerland & Sandvik, 2009). Finally, type I error rates of Welch's test ($\alpha = 0.05$) were low ($\leq 8\%$) with sample sizes similar to ours even when dealing with highly uneven sample sizes and sample variances, as well as data coming from a lognormal, beta, or exponential distribution (Algina et al., 1994).

We also assessed differences in the length frequency of lobster populations sampled from each location using two-sided Kolmogorov-Smirnov (KS) tests. Tests were performed on data combining legal (≥ 85 -mm carapace length; *P. interruptus* usually reaches sexual maturity at 65–69 mm at 5–9 years old; the maximum length caught in this study was > 150 mm) and sublegal lobsters to assess the full-size structure of the population, but additional tests were performed using only legally sized lobsters to provide consistency with catch per trap analyses. When two-sided KS tests revealed a significantly different size distribution between years for a given site ($p < 0.05$), we used one-sided KS tests and the cumulative distribution functions for the 2 years to determine which sample had a higher proportion of large lobsters.

Weights were calculated for each lobster based on sex-specific length-weight observations recorded in this study (S. Fitzgerald, unpublished data) using the allometric growth equation:

$$Wt = a(CL)^b, \quad (3)$$

where Wt refers to lobster weight (in kilograms), CL refers to lobster carapace length (in centimeters), a is a constant, and b is an allometric scaling parameter. Weights were then converted to pounds (the metric used in the lobster fishery) prior to data standardization for soak time (see above). We generated scatterplots for CPUE and weight per trap data to visualize the differences between year-

MPA–location combinations, box-and-violin plots to more accurately visualize the data spread for both variables, and histograms with superimposed density plots to visualize size data. All analyses and figure generation were performed in R (R Core Team, 2018).

RESULTS

Catch per unit effort

There were dramatic increases in legal-sized lobster CPUE within and just outside of reserve borders from 2008 to 2018 (Figure 3). The change in the spatial pattern of CPUE between the two sampling periods was indicative of a substantial increase in the spillover of legal-sized lobster from within reserves to the adjacent fishing ground. An increase in CPUE was not observed at control sites (out-far sites) located ≥ 2 km away from the reserve borders. At Gull Island Reserve (Gull), the mean number of lobsters caught per trap increased by 9.5 at in-deep sites (a 124% increase; Welch's t test: $p < 0.001$) and by 1.5 at out-edge sites (223% increase; Welch's t test: $p < 0.001$), whereas mean CPUE decreased by 0.8 lobsters per trap at out-far sites (69% decrease; Welch's t test: $p < 0.001$). Table 1 summarizes results of all statistical tests comparing CPUE between years for each combination of MPA and trap location. At Scorpion Point Reserve (Scorpion), mean CPUE increased by 20.5 at in-deep sites (402% increase; Welch's t test: $p < 0.001$), by 7.2 at in-edge sites (384% increase; Welch's t test: $p < 0.001$), and by 1.6 at out-edge sites (315% increase; Welch's t test: $p < 0.001$). CPUE did not change at in-edge sites at Gull or at out-far sites at Scorpion ($p > 0.05$ for both). Figure 3 shows mean CPUE (\pm SEs) for each year–MPA–trap location combination, and Appendix S1: Figure S1 visualizes the data spread for each combination.

A similar trend was observed for sublegal lobsters but with important differences (Appendix S1: Table S13). At Gull Island Reserve (Gull), the mean number of sublegal lobsters caught per trap increased during the 2008–2018 period by 3.2 at in-deep sites, by 1.5 at in-edge sites, but by only 0.43 at out-edge sites. At Scorpion Point Reserve (Scorpion), the mean CPUE of sublegal lobsters increased over the 10-year period by almost 6 at in-deep sites, by about 5 lobsters at in-edge sites, and by 1.3 lobsters (250%) at out-edge sites. Using the mean CPUE of both adults and sublegal lobsters for each site–year combination, we found that the ratio of sublegals to legal lobsters increased for all trapping locations except three, the out-edge at both Gull and Scorpion, and the in-deep at Scorpion (Appendix S1: Table S13).

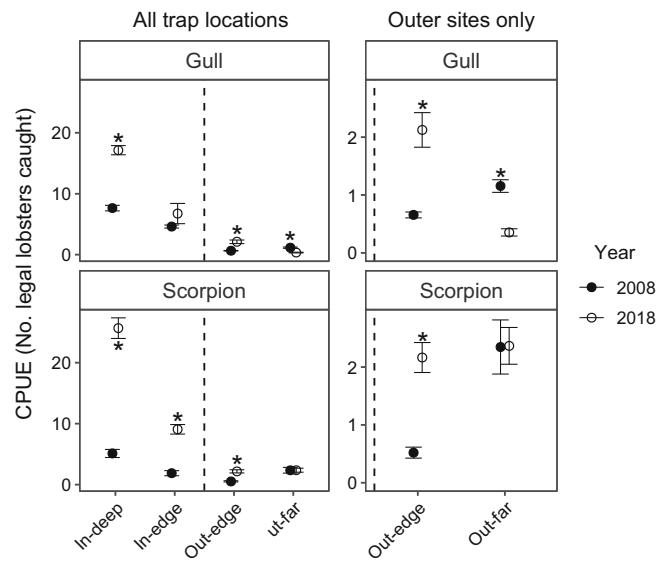


FIGURE 3 Mean catch per unit effort (CPUE; number of lobsters per trap) for every combination of year, reserve, and trap location relative to reserve borders for the Scorpion and Gull Island marine reserves. Scorpion, Scorpion Marine Reserve; Gull, Gull Island Marine Reserve. The vertical dotted line represents the reserve boundary. Open circles represent 2018 data, closed circles represent 2008 data, and error bars represent standard errors. The left panel shows data for all four trap location designations, whereas the right panel zooms in to show only data from sites outside of reserves. Asterisks next to a point indicate a significantly higher CPUE for that given year as determined by Welch's t test; * $p < 0.05$; ** $p < 0.01$; and *** $p < 0.001$. CPUE was statistically adjusted relative to soak time that is standardized in some cases, as explained in *Standardizing data for soak time*.

Weight

The increase in the total weight of lobsters caught inside reserves was even more dramatic than our measurements of CPUE (Figure 4). From 2008 to 2018 at Gull, the mean weight of lobsters caught per trap increased by 11.8 kg at in-deep sites (a 144% increase; Welch's t test: $p < 0.001$) and by 1.3 kg at out-edge sites (258% increase; Welch's t test: $p = 0.001$), whereas mean weight per trap decreased by 0.7 kg at out-far sites (74% decrease; Welch's t test: $p < 0.001$). Table 2 summarizes Welch's t test results comparing lobster weight per trap (in kilograms) between years for each combination of MPA and trap location. At Scorpion, mean weight per trap increased by 24.3 kg at in-deep sites (465% increase; Welch's t test: $p < 0.001$), by 6.13 kg at in-edge sites (335% increase; Welch's t test: $p < 0.001$), and by 1.46 kg at out-edge sites (331% increase; Welch's t test: $p < 0.001$). Like that observed for CPUE, the weight per trap did not change for in-edge sites in Gull or out-far sites at Scorpion (Welch's t test: $p > 0.05$ for both). Figure 4 shows mean

TABLE 1 Catch per unit effort (CPUE; number of lobsters per trap) for each combination of year, MPA, and trap location, including the difference between years and the associated 95% confidence interval (95% CI), and two-sided Welch's *t* test results comparing CPUE between years

Trap location	Mean CPUE		Difference (CPUE)		<i>t</i>	df	<i>p</i>	N	
	2008	2018	Mean	95% CI				2008	2018
Gull									
In-deep	7.6454949	17.1484118	9.50	7.76 to 11.25	-10.73	192.63	<0.0001	178	112
In-edge	4.6187725	6.75	2.13	-1.27 to 5.53	-1.27	40.85	0.212	263	40
Out-edge	0.6572539	2.125	1.47	0.86 to 2.08	-4.86	41.35	<0.0001	226	40
Out-far	1.1562051	0.3548387	-0.80	-1.05 to -0.56	6.41	308.87	<0.0001	221	93
Scorpion									
In-deep	5.1142857	25.6615017	20.55	16.9 to 24.19	-11.30	54.26	<0.0001	35	43
In-edge	1.8717949	9.0666667	7.19	5.45 to 8.94	-8.17	87.19	<0.0001	39	61
Out-edge	0.5211268	2.1639344	1.64	1.1 to 2.19	-5.97	151.74	<0.0001	71	122
Out-far	2.3461538	2.3653846	0.02	-1.12 to 1.16	-0.03	48.42	0.973	26	52

Note: Boldface text indicates sites with significantly greater CPUE in 2018 versus 2008. *N* denotes sample sizes in number of traps pulled. Gull, Gull Island Marine Reserve; Scorpion, Scorpion Marine Reserve (see Figure 1 for location).

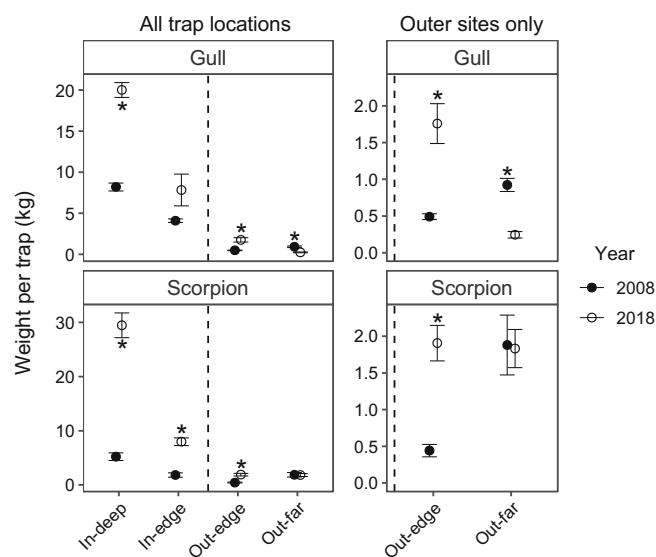


FIGURE 4 Mean lobster weight per trap (in kilograms) for every combination of year, reserve, and trap location relative to reserve borders for the Scorpion and Gull Island marine reserves. Gull, Gull Island Marine Reserve; Scorpion, Scorpion Marine Reserve. The vertical dotted line represents the reserve boundary. Open circles represent 2018 data, closed circles represent 2008 data, and error bars represent standard errors. The left panel shows data for all four trap location designations, whereas the right panel zooms in to show only data from sites outside of reserves. Asterisks next to a point indicate a significantly higher CPUE for that given year as determined by Welch's *t* test; **p* < 0.05; ***p* < 0.01; and ****p* < 0.001.

weight per trap (\pm SEs) for each year–MPA–trap location combination, and Appendix S1: Figure S2 visualizes the data spread for each combination.

Lobster size

At Gull, results of the KS tests showed that the size distributions of lobster populations (sublegals and legals combined) differed between time periods for all four sites (Table 3). There were a higher proportion of large lobsters in 2018 than in 2008 at in-deep, in-edge, and out-edge sites, and a smaller proportion of large lobsters in 2018 than in 2008 at out-far sites (one-sided $p < 0.001$ in all cases; Figure 5). These results remained similar when restricting the analysis to legal lobsters only ($p < 0.05$ in all cases; Table 3). At Scorpion, KS tests showed that the size distributions of lobster populations (sublegals and legals combined) differed for in-edge, out-edge, and out-far sites ($p < 0.05$), but not for in-deep sites ($p = 0.07$; Table 3) between 2008 and 2018 (Figure 5). There was a higher proportion of large lobster at out-edge sites in 2018 (one-sided $p = 0.01$), but a lower proportion of large lobsters in 2018 than in 2008 at in-edge and out-far sites (one-sided $p < 0.01$ for both; Table 3). When restricting analyses to legally sized lobsters, findings remained similar at in-edge and out-far sites (one-sided $p < 0.01$ for both) but were insignificant at the out-edge site ($p > 0.05$; Table 3).

DISCUSSION

Quantifying the effects of MPAs on fisheries yields is an important component of marine spatial planning, conservation, and fisheries management. Our study provides a case study on the role of marine reserves in driving

TABLE 2 Lobster weight per trap (in kilograms) for each combination of year, MPA, and trap location, including the difference between years and the associated 95% confidence interval (95% CI), and two-sided Welch's *t* test results comparing weight per trap between years

Trap location	Mean weight per trap (kg)		Difference (kg)		<i>t</i>	df	<i>p</i>	N	
	2008	2018	Mean	95% CI				2008	2018
Gull									
In-deep	8.21	20.02	11.81	9.79 to 13.84	-11.50	175.13	<0.0001	178	112
In-edge	4.10	7.84	3.74	0.19 to 7.67	-1.92	40.03	0.062	263	40
Out-edge	0.49	1.76	1.27	0.71 to 1.82	-4.62	40.69	<0.0001	226	40
Out-far	0.92	0.25	-0.68	-0.88 to -0.48	6.78	298.35	<0.0001	9	16
Scorpion									
In-deep	5.22	29.48	24.26	19.47 to 29.06	-10.16	49.65	<0.0001	221	93
In-edge	0.44	7.99	6.15	4.53 to 7.78	-7.53	90.13	<0.0001	35	43
Out-edge	0.44	1.90	1.46	2.11 to 4.33	-5.73	148.51	<0.0001	39	61
Out-far	1.88	1.83	-0.11	-0.96 to 0.93	0.10	45.90	0.921	71	122

Note: Boldface text indicates sites with significantly greater weight per trap in 2018 versus 2008. *N* denotes sample sizes in number of traps pulled. Gull, Gull Island Marine Reserve; Scorpion, Scorpion Marine Reserve (see Figure 1 for location).

fisheries yields in southern CA and offers important insight into the importance of time as a key driver in the effects of protected areas on harvest. We found that 15 years after reserves were established two key proxies for lobster population status and fishery performance (i.e., biomass and CPUE) increased substantially inside two replicate reserves, and that legal-sized lobsters were apparently spilling into nearby fished areas along the reserve borders. Our findings indicate that lobster populations may have doubled in size within reserves, and the rate of spillover may have quadrupled in the 10-year increment between 2008 and 2018. As we noted above, relatively many studies have documented the buildup of lobster populations in reserves, and the spillover of lobsters from reserves. A suite of studies has also reported that reserve-enhanced catches can increase commercial fishery yield (e.g., Goñi et al., 2011). For example, our recent work on the nearby Santa Barbara mainland coast (Lenihan et al., 2021) reported how the establishment of marine reserves in 2012 increased the yield of lobster for the commercial fishery by 200% in fishing zones near to reserves, even though the reserves removed 35% of total lobster fishing ground within those zones. In that case, the positive influence of spillover on yield was observed within 6 years of the establishment of reserves. By contrast, here we report that more than twice that amount of time was necessary to enhance catch outside of reserves in the NCI, specifically on Santa Cruz Island, which is located about 40 km from the mainland.

Two factors help explain the delayed response in spillover in the NCI compared with that observed for mainland reserves. First, the fishery on the mainland is much

more intensively fished than in the NCI (Guenther et al., 2015), which is logical because the NCI is much farther away from the Santa Barbara Harbor than the local coastal fishery. As such, there are twofold to three-fold more traps placed annually along the mainland than in NCI (CDFW, 2019). The result is relatively less heavily fished populations in the NCI, which theory predicts should lead to relatively less spillover (Hilborn et al., 2004). In addition, it was not until relatively recently (since ~2008) that lobster fishers began substantially fishing the line in the NCI, whereas they began to fish the line almost immediately after the mainland reserve was established in 2012, perhaps due to an evolution of fishing behavior in the NCI. Second, the reserves producing substantial spillover on the mainland were connected in space to nearby fishing grounds by the continuous rocky reef habitat across which lobster readily move (Lenihan et al., 2021). The mainland reefs probably provided safe passage for lobsters out of reserves where they eventually were caught. Conversely, the border region of two reserves sampled in the NCI in this study contained reefs distributed in patches across substantial areas of the sand bottom, over which lobsters prefer not to travel (Goñi et al., 2008; Kay, Lenihan, Kotchen, & Miller, 2012). In combination, these two factors probably delayed both the fishery-driven development of a steep gradient in lobster abundance from inside to outside reserve borders—a gradient indicative of spillover (Halpern et al., 2009; Kellner et al., 2007)—and the rate of movement of lobsters from areas of high population density within the reserves to relatively low population density outside of the reserves.

TABLE 3 Kolmogorov–Smirnov (KS) test results comparing length frequencies of lobsters between years for each combination of MPA and trap location

Trap location	<i>D</i>	<i>p</i>	Test	CDF interpretation	<i>N</i>	
					2008	2018
All lobsters (legal + sublegal combined)						
Gull						
In-deep	0.174	<0.0001	One-sided	Larger lobsters in 2018	2252	1705
In-edge	0.264	<0.0001	One-sided	Larger lobsters in 2018	2808	389
Out-edge	0.189	<0.0001	One-sided	Larger lobsters in 2018	811	175
Out-far	0.169**	0.001	One-sided	<i>Smaller lobsters in 2018**</i>	1064	151
Scorpion						
In-deep	0.083	0.067	Two-sided	N.S.	311	1156
In-edge	0.231**	<0.0001	One-sided	<i>Smaller lobsters in 2018**</i>	101	723
Out-edge	0.148	0.012	One-sided	Larger lobsters in 2018	125	530
Out-far	0.179**	0.004	One-sided	<i>Smaller lobsters in 2018**</i>	128	265
Legal lobsters only						
Gull						
In-deep	0.237	<0.0001	One-sided	Larger lobsters in 2018	579	429
In-edge	0.375	<0.0001	One-sided	Larger lobsters in 2018	380	99
Out-edge	0.187	0.012	One-sided	Larger lobsters in 2018	66	57
Out-far	0.251**	0.022	One-sided	<i>Smaller lobsters in 2018**</i>	187	17
Scorpion						
In-deep	0.096	0.111	Two-sided	N.S.	127	492
In-edge	0.232**	0.001	One-sided	<i>Smaller lobsters in 2018**</i>	45	156
Out-edge	0.180	0.159	Two-sided	N.S.	36	157
Out-far	0.260**	0.002	One-sided	<i>Smaller lobsters in 2018**</i>	61	67

Note: *D* is the test statistic; “Test” indicates whether the results are for a one-sided or two-sided test; “CDF interpretation” refers to a comparison of the cumulative distribution functions (CDFs) between years to determine which year yielded larger lobsters; and *N* denotes sample size (number of lobsters measured) in each year. The top panel presents results from analyses that included all lobsters, whereas the bottom panel presents results from analyses restricted to only legal lobsters. Boldface text indicates a significantly higher proportion of large lobsters in 2018, whereas asterisks and italic text indicate a significantly smaller proportion of large lobsters in 2018. Gull, Gull Island Marine Reserve; Scorpion, Scorpion Marine Reserve (see Figure 1 for location).

We are confident that the patterns that we observed in our trapping data indicate spillover contributions to the southern CA lobster fishery. Several reasons underlie our confidence. First, lobster fishers now intently focus on fishing at reserve borders in the CINMS, including at the Gull Island and Scorpion Point reserves, and elsewhere throughout the SBC ecosystem (Lenihan et al., 2021; C. Voss, personal communication). Fishers sample continually with their traps to identify the best harvest locations and have strong economic incentives to fish in the most productive spots. According to our fishing partners, fishing has increased at reserve borders as the catch rates have increased in those locations over the past 10 years. The most reasonable explanation for greater catch rates through time at reserve borders is the buildup and subsequent spillover of lobsters from no-fishing

reserves. Second, we have no evidence that natural variation through space in lobster abundance drove the patterns that we observed. In fact, our work from 2003 to 2008 indicated lobster abundance was similar across all sites prior to reserve establishment and increased inside of reserves after fishing ceased.

Whether spatial variation in recruitment drove the patterns that we report is possible but not supported by our data. We have and know of no data on recruitment. Instead, we collected CPUE for sublegal lobsters that provide a proxy for recruitment (Kay, Lenihan, Guenther, et al., 2012). Those data (see Appendix S1: Table S13) indicate that the CPUE of sublegals increased everywhere (except one site; out-far at Gull Island), thus implying that recruitment may have increased ubiquitously across the CINMS. That recruitment may have

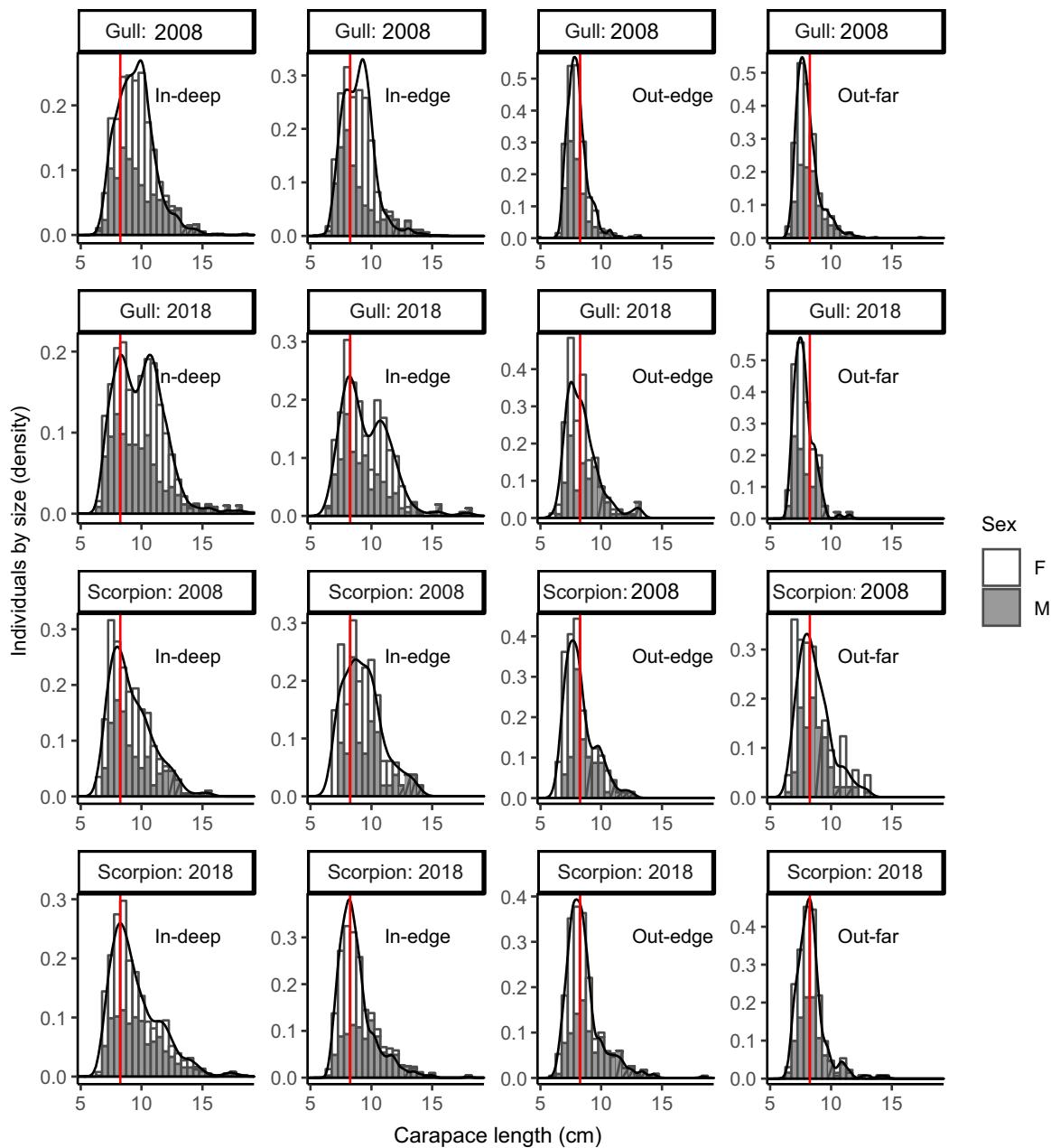


FIGURE 5 Length frequency (carapace length, cm) of sampled lobster populations for each combination of year (1st and 3rd row = 2008, 2nd and 4th row = 2018), reserve (top two rows = Gull marine reserve; bottom two rows = Scorpion marine reserve), and trap location (from left to right: in-deep, in-edge, out-edge, out-far). Males (M) are shown in dark gray and females (F) are shown in white. Red line is the carapace length of a legal-size lobster. Rectangles indicate histogram bins and pink shading reflects density plots for both sexes combined.

increased at the highest rates within the reserves is also possible, as the level of anthropogenic disturbances also generally decreased in reserves, habitat improved, and lobster recruitment may be gregarious to some degree. Furthermore, the ratio of sublegal to legal lobsters (Appendix S1: Table S13), in theory, implies indirectly that spillover increased. With a net movement of adult lobsters out of reserves, and under the assumption that smaller sublegals move less than adults, even with

greater density-dependent interactions, one might predict that the ratio of sublegals to legals increases with greater spillover. Data in Appendix S1: Table S13 support this theory, as 70% of the locations that we sampled had a higher sublegal: legal ratio in 2018 than in 2008. Why the ratio declined over this period at Scorpion “in-deep” appears to be the substantially large increase in legal lobster toward the middle of the reserve. Nevertheless, we caught more sublegals at that site in 2018 than in 2008.

That the ratio declined at the out-edge site is entirely consistent with an increase in spillover, especially because the CPUE of sublegals also went up at that site during the same period. Certainly, recruitment variation may have been a contributing factor influencing our results, but we think it does not confound our study and weaken our conclusion that greater spillover generated greater catch rates at the borders of the two reserves. Third, we did not conduct a tagging study that would have provided additional evidence for or against enhanced spillover. However, Kay, Lenihan, Guenther, et al. (2012) did conduct a tagging study and their conclusion was that by 2008, 5 years after reserves were established, that lobsters were moving in and out of reserves, and that the movement combined with the pattern of catches supported the presence of spillover, albeit at not high enough rates to stimulate the fishery to fish the borders (see also Guenther et al., 2015). The pattern of fishing has radically changed since then. Finally, if the substantial increases in the preseason weight per trap that we report were a result of broadscale environmental changes, landings probably would have increased uniformly across the fishery. However, trap yield did not increase at out-far control sites, confirming that increased weight per trap in and near reserve borders was a reserve-based effect. The direction and statistical significance of results also remained the same when using raw data not standardized for soak time (see Appendix S1: Tables S11 and S12). In summary, we detected clear evidence of substantial levels of spillover occurring in the Channel Islands CA (NCI) spiny lobster fishery 15 years after reserves were established. The economic implications of spillover may be significant for the fishery, but future research efforts are required to fully assess these economic consequences.

The roughly fourfold increase in weight per trap of lobsters caught in our experimental fishing at the outer edge of reserves reflects a considerable contribution of MPAs to the adjacent fishery. At-sea observations from the last week of sampling confirmed that fishers are taking advantage of spillover by placing high numbers of traps near reserve borders (i.e., fishing the line), contrary to fisher behavior in 2008 and before (Guenther et al., 2015). The true magnitude of spillover benefits experienced by local fishers may also be higher than estimated here because August and September are months where spiny lobsters at the Channel Islands are not particularly mobile, in part because this is when they molt so are most vulnerable to predators. CA spiny lobsters appear to undergo offshore–nearshore migrations beginning in late October, and winter storms cause increased movement rates as well (CDFG, 2004, 2013; Kay, Lenihan, Guenther, et al., 2012). Fishers move their traps

further offshore later in the fishing season to take advantage of these migrations (CDFW, 2013), representing an additional opportunity to benefit from spillover. Substantial fishery enhancement may also be occurring via larval spillover, a key component of MPA benefits to surrounding fisheries that we did not consider in this study (Botsford et al., 2009; Guénette et al., 1998). Finally, the 144%–465% increase in weight per trap deep within reserves augments a previously detected fourfold to eightfold increase in trap yield at these same sites between 1998 and 2002 and between 2007 and 2008 (Kay, Lenihan, Guenther, et al., 2012), suggesting that biomass levels deep inside reserves in 2018 may be approximately 20 times prereserve levels.

A 20-fold increase in lobster biomass in reserves is larger than that detected in most empirical studies (Follesø et al., 2011; Jack & Wing, 2010; Moland et al., 2013), but is within expected ranges for reserves that have been protected for over 15 years (Kelly et al., 2000; Shears et al., 2006). Nevertheless, results from this study are novel because stock assessment determined that the CA spiny lobster fishery was sustainable from 2000 onward (Neilson, 2011). The increased trap yield at out-edge sites also occurred despite a reported 34% increase in fishing effort (number of traps pulled) in the 10 fishing blocks closest to Santa Cruz Island from 1998–2003 to 2013–2017 (CDFW, 2019). To our knowledge, this is the first study to document dramatic reserve-driven increases in trap yield outside MPA borders in a fishery that was already considered sustainable prior to MPA implementation.

Whether the level of spillover we detected in this study offsets the cost of losing approximately one fifth of the viable fishing grounds at the Channel Islands due to MPA establishment (Guenther et al., 2015; Kay, Lenihan, Guenther, et al., 2012) remains an important question to address. Marine protected areas are often promoted as devices that will lead to increased long-term yields, but such advocacy can sometimes be unqualified and misleading, thereby leading to negative perceptions of reserves and friction between fishers, scientists, and managers (Agardy et al., 2003; Bennett & Dearden, 2014; Hilborn et al., 2004). Individual reserves must be monitored and evaluated over time to maintain credibility and transparency between managers and stakeholders (Hilborn et al., 2004). For CA spiny lobster, the next challenge is to assess the overall benefit spillover has on the fishery based in part on the information generated from this study. Our results are vital because they demonstrate the value of MPAs as a fishery management tool for CA spiny lobster, and the need for monitoring and evaluating reserve success over the long term (see also Gerber et al., 2005).

Honoring Charles H. Peterson (1946–2020)

This paper was inspired by our colleague and mentor Professor Charles H. “Pete” Peterson, who for over four decades, beginning in the early 1970s, worked to solve marine environmental problems while simultaneously advancing the field of ecology. Pete’s research, teaching, and leadership helped reposition applied marine ecology to the forefront of marine science. Following his advice, we utilized a robust experimental trapping design that controlled for fine-scale habitat features, broadscale environmental changes, and fishing activity to compare catch per trap 5 and 15 years after reserve implementation. Establishing and repeating well-designed field studies are critical for learning whether management actions, such as establishing MPAs, are meeting their intended goals and objectives. Following in Pete’s footsteps, we have shown that MPAs in the SBC are meeting important management goals for the CA spiny lobster fishery.

ACKNOWLEDGMENTS

This work was inspired by and executed in honor of Professor Charles H. Peterson (1946–2020). We could not have conducted the work without the expert advice of Dr Matthew C. Kay and Chris Voss, a commercial lobster fisher, who provided the vessel, equipment, and LEK enabling us to conduct the study, and who worked in the field with us to help sample. Funding for this research was provided by the National Science Foundation’s support of the Santa Barbara Coastal Long Term Ecological Research program (NSF OCE 1831937), California Sea Grant Prop 84 grant program (R/OPCOAH-2), the Environmental Markets Solution Laboratory (emLAB) at UC Santa Barbara, and Ocean Recoveries Lab at UC Santa Barbara. All methods were carried out in accordance with the University of California and National Science Foundation guidelines and regulations. All experimental protocols were approved by the University of California, Santa Barbara, and the California Department of Fish and Wildlife.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

A portion of the data (from 2008) was published previously (Kay, Lenihan, Kotchen, & Miller, 2012). The 2018 data and all analytical codes (Santa Barbara Coastal LTER and Lenihan, 2021) are available from the Environmental Data Initiative (EDI) Data Portal: <https://doi.org/10.6073/pasta/69929b35dcffc7014ac47c72db06cb3e>.

ORCID

Adrian C. Stier  <https://orcid.org/0000-0002-4704-4145>

REFERENCES

- Agardy, T., P. Bridgewater, M. P. Crosby, J. Day, P. K. Dayton, R. Kenchington, D. Laffoley, et al. 2003. “Dangerous Targets? Unresolved Issues and Ideological Clashes around Marine Protected Areas.” *Aquatic Conservation: Marine and Freshwater Ecosystems* 13: 353–67.
- Algina, J., T. C. Oshima, and W. Y. Lin. 1994. “Type I Error Rates for Welch’s Test and James’s Second-Order Test under Non-normality and Inequality of Variance When There Are Two Groups.” *Journal of Educational Statistics* 19: 275–91.
- Babcock, R. C., S. Kelly, N. T. Shears, J. W. Walker, and T. J. Willis. 1999. “Changes in Community Structure in Temperate Marine Reserves.” *Marine Ecology Progress Series* 189: 125–34.
- Bennett, N. J., and P. Dearden. 2014. “Why Local People Do Not Support Conservation: Community Perceptions of Marine Protected Area Livelihood Impacts, Governance and Management in Thailand.” *Marine Policy* 44: 107–16.
- Bevacqua, D., P. Melià, M. C. Follesa, G. A. De Leo, M. Gatto, and A. Cau. 2010. “Body Growth and Mortality of the Spiny Lobster *Palinurus elephas* within and outside a Small Marine Protected Area.” *Fisheries Research* 106: 543–9.
- Botsford, L. W., D. R. Brumbaugh, C. Grimes, J. B. Kellner, J. Largier, J., M. R. O’Farrell, S. Ralston, E. Soulanille, and V. Wespestad. 2009. “Connectivity, Sustainability, and Yield: Bridging the Gap between Conventional Fisheries Management and Marine Protected Areas.” *Reviews in Fish Biology and Fisheries* 19: 69–95.
- Byers, J. E. 2005. “Marine Reserves Enhance Abundance but Not Competitive Impacts of a Harvested Nonindigenous Species.” *Ecology* 86: 487–500.
- Byers, J. E., and E. G. Noonburg. 2007. “Poaching, Enforcement, and the Efficacy of Marine Reserves.” *Ecological Applications* 17: 1851–6.
- California Department of Fish and Game. 2004. “California Spiny Lobster.” In *Annual Status of the Fisheries Report through 2003*, edited by C. Ryan and N. Payten, 4-1–4-12. Monterey, CA: California Department of Fish and Wildlife, Marine Region.
- California Department of Fish and Game, Partnership for Interdisciplinary Studies of Coastal Oceans, Channel Islands National Marine Sanctuary, and Channel Islands National Park. 2008. In *Channel Islands Marine Protected Areas: First 5 Years of Monitoring: 2003–2008*, edited by S. Airamé and J. Ugoretz. Monterey, CA: California Department of Fish and Wildlife, Marine Region.
- California Department of Fish and Wildlife. 2013. “California Spiny Lobster, *Panulirus interruptus*.” In *Status of the Fisheries Report: An Update Through 2011*, edited by T. Larinto, 1-1–9. Monterey, CA: California Department of Fish and Wildlife, Marine Region.
- California Department of Fish and Wildlife. 2019. *Confidential Logbook Data by Fishing Block for CA Spiny Lobster, 1998–2017*. Monterey, CA: California Department of Fish and Wildlife, Marine Region.
- Caselle, J. E., A. Rassweiler, S. L. Hamilton, and R. R. Warner. 2015. “Recovery Trajectories of Kelp Forest Animals Are Rapid

- Yet Spatially Variable across a Network of Temperate Marine Protected Areas.” *Scientific Reports* 5: 14102.
- De Leo, G. A., and F. Micheli. 2015. “The Good, the Bad and the Ugly of Marine Reserves for Fishery Yields.” *Philosophical Transactions of the Royal Society B: Biological Sciences* 370: 20140276.
- Di Franco, A., P. Thiriet, G. Di Carlo, C. Dimitriadis, P. Francour, N. L. Gutiérrez, A. J. De Grissac, et al. 2016. “Five Key Attributes Can Increase Marine Protected Areas Performance for Small-Scale Fisheries Management.” *Scientific Reports* 6: 38135.
- Di Lorenzo, M., J. Claudet, and P. Guidetti. 2016. “Spillover from Marine Protected Areas to Adjacent Fisheries Has an Ecological and a Fishery Component.” *Journal for Nature Conservation* 32: 62–6.
- Di Lorenzo, M., P. Guidetti, A. Di Franco, A. Calò, and J. Claudet. 2020. “Assessing Spillover from Marine Protected Areas and its Drivers: A Meta-Analytical Approach.” *Fish and Fisheries* 21: 906–15.
- Edgar, G. J., and N. S. Barrett. 1999. “Effects of the Declaration of Marine Reserves on Tasmanian Reef Fishes, Invertebrates and Plants.” *Journal of Experimental Marine Biology and Ecology* 242: 107–44.
- Egginton, D. B., and D. M. Parsons. 2008. “Disturbance-Induced ‘Spill-in’ of Caribbean Spiny Lobster to Marine Reserves.” *Marine Ecology Progress Series* 371: 213–20.
- Fagerland, M. W., and L. Sandvik. 2009. “Performance of Five Two-Sample Location Tests for Skewed Distributions with Unequal Variances.” *Contemporary Clinical Trials* 30: 490–6.
- Follesø, M. C., R. Cannas, A. Cau, D. Cuccu, A. Gastoni, A. Ortú, C. Pedoni, C. Porcu, and A. Cau. 2011. “Spillover Effects of a Mediterranean Marine Protected Area on the European Spiny Lobster *Palinurus elephas* (Fabricius, 1787) Resource.” *Aquatic Conservation: Marine and Freshwater Ecosystems* 21: 564–72.
- Freeman, D. J., A. B. MacDiarmid, and R. B. Taylor. 2009. “Habitat Patches that Cross Marine Reserve Boundaries: Consequences for the Lobster *Jasus edwardsii*.” *Marine Ecology Progress Series* 388: 159–67.
- Gell, F. R., and C. M. Roberts. 2003. “Benefits beyond Boundaries: The Fishery Effects of Marine Reserves.” *Trends in Ecology & Evolution* 18: 448–55.
- Gerber, L. R., M. Beger, M. A. McCarthy, and H. P. Possingham. 2005. “A Theory for Optimal Monitoring of Marine Reserves.” *Ecology Letters* 8: 829–37.
- Goñi, R., S. Adlerstein, D. Alvarez-Berastegui, A. Forcada, O. Reñones, G. Criquet, S. Polti, et al. 2008. “Spillover from Six Western Mediterranean Marine Protected Areas: Evidence from Artisanal Fisheries.” *Marine Ecology Progress Series* 366: 159–74.
- Goñi, R., F. Badalamenti, and M. H. Tupper. 2011. “Effects of Marine Protected Areas on Local Fisheries: Evidence from Empirical Studies.” In *Marine Protected Areas: A Multidisciplinary Approach*, edited by J. Claudet, 73–102. Cambridge: Cambridge University Press.
- Goñi, R., R. Hilborn, D. Díaz, S. Mallol, and S. Adlerstein. 2010. “Net Contribution of Spillover from a Marine Reserve to Fishery Catches.” *Marine Ecology Progress Series* 400: 233–43.
- Goñi, R., A. Quetglas, and O. Reñones. 2006. “Spillover of Spiny Lobsters *Palinurus elephas* from a Marine Reserve to an Adjoining Fishery.” *Marine Ecology Progress Series* 308: 207–19.
- Guénette, S., T. Lauck, and C. Clark. 1998. “Marine Reserves: From Beverton and Holt to the Present.” *Reviews in Fish Biology and Fisheries* 8: 251–72.
- Guenther, C. 2010. “A Socio-Ecological Analysis of Marine Protected Areas and Commercial Lobster Fishing in the Santa Barbara Channel, California.” Dissertation, University of California.
- Guenther, C., D. López-Carr, and H. S. Lenihan. 2015. “Differences in Lobster Fishing Effort before and after MPA Establishment.” *Applied Geography* 59: 78–87.
- Halpern, B. S., S. E. Lester, and J. B. Kellner. 2009. “Spillover from Marine Reserves and the Replenishment of Fished Stocks.” *Environmental Conservation* 36: 268–76.
- Halpern, B. S., S. E. Lester, and K. L. McLeod. 2010. “Placing Marine Protected Areas onto the Ecosystem-Based Management Seascape.” *Proceedings of the National Academy of Sciences* 107: 18312–7.
- Hilborn, R., F. Micheli, and G. A. De Leo. 2006. “Integrating Marine Protected Areas with Catch Regulation.” *Canadian Journal of Fisheries and Aquatic Sciences* 63: 642–9.
- Hilborn, R., K. Stokes, J. J. Maguire, T. Smith, L. W. Botsford, M. Mangel, J. Orensanz, et al. 2004. “When Can Marine Reserves Improve Fisheries Management?” *Ocean and Coastal Management* 47: 197–205.
- Hoskin, M. G., R. A. Coleman, E. Von Carlshausen, and C. M. Davis. 2011. “Variable Population Responses by Large Decapod Crustaceans to the Establishment of a Temperate Marine No-Take Zone.” *Canadian Journal of Fisheries and Aquatic Sciences* 68: 185–200.
- Jack, L., and S. R. Wing. 2010. “Maintenance of Old-Growth Size Structure and Fecundity of the Red Rock Lobster *Jasus edwardsii* among Marine Protected Areas in Fiordland, New Zealand.” *Marine Ecology Progress Series* 404: 161–72.
- Jennings, S. 2000. “Patterns and Prediction of Population Recovery in Marine Reserves.” *Reviews in Fish Biology and Fisheries* 10: 209–31.
- Jiao, J., S. S. Pilyugin, L. Riote-Lambert, and C. W. Osenberg. 2018. “Habitat-Dependent Movement Rate Can Determine the Efficacy of Marine Protected Areas.” *Ecology* 99: 2485–95.
- Kaplan, K. A., L. Yamane, L. W. Botsford, M. L. Baskett, A. Hastings, S. Worden, and J. W. White. 2019. “Setting Expected Timelines of Fished Population Recovery for the Adaptive Management of a Marine Protected Area Network.” *Ecological Applications* 29: e01949.
- Kay, M. C., H. S. Lenihan, C. M. Guenther, J. R. Wilson, C. J. Miller, and S. W. Shrout. 2012. “Collaborative Assessment of California Spiny Lobster Population and Fishery Responses to a Marine Reserve Network.” *Ecological Applications* 22: 322–35.
- Kay, M. C., H. S. Lenihan, M. J. Kotchen, and C. J. Miller. 2012. “Effects of Marine Reserves on California Spiny Lobster Are Robust and Modified by Fine-Scale Habitat Features and Distance from Reserve Borders.” *Marine Ecology Progress Series* 451: 137–50.
- Kay, M. C., and J. R. Wilson. 2012. “Spatially Explicit Mortality of California Spiny Lobster (*Panulirus interruptus*) across a Marine Reserve Network.” *Environmental Conservation* 39: 215–24.

- Kellner, J. B., I. Tetreault, S. D. Gaines, and R. M. Nisbet. 2007. "Fishing the Line near Marine Reserves in Single and Multi-species Fisheries." *Ecological Applications* 17: 1039–54.
- Kelly, S., D. Scott, A. B. MacDiarmid, and R. C. Babcock. 2000. "Spiny Lobster, *Jasus edwardsii*, Recovery in New Zealand Marine Reserves." *Biological Conservation* 92: 359–69.
- Kerwath, S. E., H. Winker, A. Götz, and C. G. Attwood. 2013. "Marine Protected Area Improves Yield without Disadvantaging Fishers." *Nature Communications* 4: 2347.
- Kramer, D. L., and M. R. Chapman. 1999. "Implications of Fish Home Range Size and Relocation for Marine Reserve Function." *Environmental Biology of Fishes* 55: 65–79.
- Le Quesne, W. J., and E. A. Codling. 2008. "Managing Mobile Species with MPAs: The Effects of Mobility, Larval Dispersal, and Fishing Mortality on Closure Size." *ICES Journal of Marine Science* 66: 122–31.
- Lenihan, H. S., J. P. Gallagher, J. R. Peters, A. C. Stier, J. K. K. Hofmeister, and D. C. Reed. 2021. "Evidence that Spillover from Marine Protected Areas Benefits the Spiny Lobster (*Panulirus interruptus*) Fishery in Southern California." *Scientific Reports* 11: 2663.
- Lester, S. E., B. S. Halpern, K. Grorud-Colvert, J. Lubchenco, B. I. Ruttenberg, S. D. Gaines, S. Airame, and R. R. Warner. 2009. "Biological Effects within No-Take Marine Reserves: A Global Synthesis." *Marine Ecology Progress Series* 384: 33–46.
- Ley-Cooper, K., S. De Lestang, B. F. Phillips, and E. Lozano-Álvarez. 2014. "An Unfished Area Enhances a Spiny Lobster, *Panulirus argus*, Fishery: Implications for Management and Conservation within a Biosphere Reserve in the Mexican Caribbean." *Fisheries Management and Ecology* 21: 264–74.
- Lubchenco, J., S. R. Palumbi, S. D. Gaines, and S. Andelman. 2003. "Plugging a Hole in the Ocean: The Emerging Science of Marine Reserves." *Ecological Applications* 13(Special Issue): 3–7.
- Lynam, J., A. Nikolaev, J. Raynor, T. Vilela, and J. C. Villaseñor-Derbez. 2020. "Impact of Two of the World's Largest Protected Areas on Longline Fishery Catch Rates." *Nature Communications* 11: 1–9.
- McClanahan, T. R. 1999. "Is there a Future for Coral Reef Parks in Poor Tropical Countries?" *Coral Reefs* 18: 321–5.
- Moffitt, E. A., L. W. Botsford, D. M. Kaplan, and M. R. O'Farrell. 2009. "Marine Reserve Networks for Species that Move within a Home Range." *Ecological Applications* 19: 1835–47.
- Moland, E., E. M. Olsen, K. Andvord, J. A. Knutsen, and N. C. Stenseth. 2011. "Home Range of European Lobster (*Homarus gammarus*) in a Marine Reserve: Implications for Future Reserve Design." *Canadian Journal of Fisheries and Aquatic Sciences* 68: 1197–210.
- Moland, E., E. M. Olsen, H. Knutsen, P. Garrigou, S. H. Espeland, A. R. Kleiven, C. Andre', and J. A. Knutsen. 2013. "Lobster and Cod Benefit from Small-Scale Northern Marine Protected Areas: Inference from an Empirical Before-After Control-Impact Study." *Proceedings of the Royal Society B: Biological Sciences* 280: 20122679.
- Neilson, D. J.. 2011. Assessment of the California Spiny Lobster (*Panulirus interruptus*). Final, Post Technical Review, Report Submitted to and Approved by the California Fish and Game Commission.
- Parrish, R. 1999. "Marine Reserves for Fisheries Management: Why Not." *Reports of California Cooperative Oceanic Fisheries Investigations* 40: 77–86.
- Pelc, R. A., R. R. Warner, S. D. Gaines, and C. B. Paris. 2010. "Detecting Larval Export from Marine Reserves." *Proceedings of the National Academy of Sciences* 107: 18266–71.
- R Core Team. 2018. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing. <https://www.R-project.org/>.
- Roberts, C. M., J. P. Hawkins, and F. R. Gell. 2005. "The Role of Marine Reserves in Achieving Sustainable Fisheries." *Philosophical Transactions of the Royal Society B: Biological Sciences* 360: 123–32.
- Rowe, S. 2002. "Population Parameters of American Lobster inside and outside No-Take Reserves in Bonavista Bay, Newfoundland." *Fisheries Research* 56: 167–75.
- Russ, G. R., and A. C. Alcala. 2011. "Enhanced Biodiversity beyond Marine Reserve Boundaries: The Cup Spillith over." *Ecological Applications* 21: 241–50.
- Ruxton, G. D. 2006. "The Unequal Variance *t*-Test Is an Underused Alternative to Student's *t*-Test and the Mann-Whitney *U* Test." *Behavioral Ecology* 17: 688–90.
- Sala, E., and S. Giakoumi. 2017. "No-Take Marine Reserves Are the Most Effective Protected Areas in the Ocean." *ICES Journal of Marine Science* 75: 1166–8.
- Sale, P. F., R. K. Cowen, B. S. Danilowicz, G. P. Jones, J. P. Kritzer, K. C. Lindeman, S. Planes, et al. 2005. "Critical Science Gaps Impede Use of No-Take Fishery Reserves." *Trends in Ecology & Evolution* 20: 74–80.
- Santa Barbara Coastal LTER and H. Lenihan. 2021. "SBC LTER: Theme 1B: Lobster Trap Data from Marine Reserves Version 1." Environmental Data Initiative. <https://doi.org/10.6073/pasta/69929b35dcffc7014ac47c72db06cb3e>
- Shears, N. T., R. V. Grace, N. R. Usmar, V. Kerr, and R. C. Babcock. 2006. "Long-Term Trends in Lobster Populations in a Partially Protected Vs. No-Take Marine Park." *Biological Conservation* 132: 222–31.
- Thorbjørnsen, S. H., E. Moland, M. B. O. Huserbråten, J. A. Knutsen, H. Knutsen, and E. M. Olsen. 2018. "Replicated Marine Protected Areas (MPAs) Support Movement of Larger, but Not More, European Lobsters to Neighbouring Fished Areas." *Marine Ecology Progress Series* 595: 123–33.
- Walters, C. J., R. Hilborn, and R. Parrish. 2007. "An Equilibrium Model for Predicting the Efficacy of Marine Protected Areas in Coastal Environments." *Canadian Journal of Fisheries and Aquatic Sciences* 64: 1009–18.
- White, J. W., L. W. Botsford, A. Hastings, M. L. Baskett, D. M. Kaplan, and L. A. Barnett. 2013. "Transient Responses of Fished Populations to Marine Reserve Establishment." *Conservation Letters* 6: 180–91.
- White, J. W., M. T. Yamane, K. J. Nickols, and J. E. Caselle. 2020. "Analysis of Fish Population Size Distributions Confirms Cessation of Fishing in Marine Protected Areas." *Conservation Letters* 14(2): e12775.
- Willis, T. J., R. B. Millar, and R. C. Babcock. 2003. "Protection of Exploited Fish in Temperate Regions: High Density and Biomass of Snapper *Pagrus auratus* (Sparidae) in Northern New Zealand Marine Reserves." *Journal of Applied Ecology* 40: 214–27.

- Withy-Allen, K. R., and K. A. Hovel. 2013. "California Spiny Lobster (*Panulirus interruptus*) Movement Behavior and Habitat Use: Implications for the Effectiveness of Marine Protected Areas." *Marine and Freshwater Research* 64: 359–71.
- Woodcock, P., B. C. O'Leary, M. J. Kaiser, and A. S. Pullin. 2017. "Your Evidence or Mine? Systematic Evaluation of Reviews of Marine Protected Area Effectiveness." *Fish and Fisheries* 18: 668–81.
- Zimmerman, D. W., and B. D. Zumbo. 1993. "Rank Transformations and the Power of the Student t test and Welch t' test for Non-normal Populations with Unequal Variances." *Canadian Journal of Experimental Psychology/Revue Canadienne de Psychologie Expérimentale* 47: 523.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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