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Collaborative assessment of California spiny lobster population and fishery responses to a marine reserve network

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Abstract. Assessments of the conservation and fisheries effects of marine reserves typically focus on single reserves where sampling occurs over narrow spatiotemporal scales. A strategy for broadening the collection and interpretation of data is collaborative fisheries research (CFR). Here we report results of a CFR program formed in part to test whether reserves at the Santa Barbara Channel Islands, USA, influenced lobster size and trap yield, and whether abundance changes in reserves led to spillover that influenced trap yield and effort distribution near reserve borders. Industry training of scientists allowed us to sample reserves with fishery relevant metrics that we compared with pre-reserve fishing records, a concurrent port sampling program, fishery effort patterns, the local ecological knowledge (LEK) of fishermen, and fishery-independent visual surveys of lobster abundance. After six years of reserve protection, there was a four- to eightfold increase in trap yield, a 5–10% increase in the mean size (carapace length) of legal sized lobsters, and larger size structure of lobsters trapped inside vs. outside of three replicate reserves. Patterns in trap data were corroborated by visual scuba surveys that indicated a four- to sixfold increase in lobster density inside reserves. Population increases within reserves did not lead to increased trap yields or effort concentrations (fishing the line) immediately outside reserve borders. The absence of these catch and effort trends, which are indicative of spillover, may be due to moderate total mortality ($Z = 0.59$ for legal sized lobsters outside reserves), which was estimated from analysis of growth and length frequency data collected as part of our CFR program. Spillover at the Channel Islands reserves may be occurring but at levels that are insufficient to influence the fishery dynamics that we measured. Future increases in fishing effort (outside reserves) and lobster biomass (inside reserves) are likely and may lead to increased spillover, and CFR provides an ideal platform for continued assessment of fishery–reserve interactions.

Key words: California spiny lobster; collaborative fisheries research; ecosystem-based management; effort; fishery dependence; fishing the line; LEK (local ecological knowledge); mortality; Panulirus interruptus; spillover; yield.

INTRODUCTION

Humans depend substantially on the protein and economic revenues generated by marine fishing. Concern for the sustainability of fishing industries and the ecosystems upon which they depend has increased in recent decades due to depletion of fish stocks (Pauly et al. 2002, Hilborn et al. 2003, Myers and Worm 2003), evidence of resource collapse (Myers et al. 1997, Mullon et al. 2005), and perceived management failure (Pew 2003). These suboptimal human–resource interactions impact socioeconomics (Hamilton and Otterstad 1998, Milich 1999), as well as marine ecosystems (Pauly et al. 1998, Jackson et al. 2001, Lotze et al. 2006). Although the scale of the fisheries problem is subject to debate (Caddy et al. 1998, Walters 2003, Hampton et al. 2005,

Murawski et al. 2007, Sethi et al. 2010, Branch et al. 2011), there is widespread perception that management must embrace new strategies for improved stewardship of human and natural systems (UN 2002, Lubchenco et al. 2003, FAO 2007).

Marine reserves that prohibit consumptive activities are common globally and have the potential to simultaneously protect ecosystems and fisheries (UNEP-WCMC 2008). Empirical studies indicate that marine reserves are generally effective conservation tools that increase the abundance and mean size of organisms within reserve borders, especially those organisms targeted by local fisheries (reviews by Côté et al. 2001, Halpern 2003, Lester et al. 2009). However, most studies proceed with considerable and often unaddressed uncertainty due to lack of replication (at the reserve level), the absence of data prior to reserve implementation, and the collection of data over small spatial scales (Osenberg et al. 2006). These shortcomings are under-

standable because many reserves are designated as single areas and/or on political timetables that preclude scientific sampling prior to establishment. Regardless, many assessments do not control for generally high spatiotemporal variability in ecological processes, and the environmental drivers, that contribute to real or perceived reserve effects (Willis et al. 2003, Sale et al. 2005). Reserve studies focused on spiny lobster indicate that population increases are common inside reserves (MacDiarmid and Breen 1993, Edgar and Barrett 1997, 1999, Kelly et al. 2000, Goñi et al. 2001), but such increases are not ubiquitous (MacDiarmid 1991, Mac-Diarmid and Breen 1993, Acosta 2001, Lipcius et al. 2001, Marí et al. 2002, Mayfield et al. 2005), and they provide a cautionary example regarding the generality of reserve effects and the need for spatiotemporal coverage in assessments.

An important mechanism by which reserves influence fisheries is the movement of adult animals from within reserves to adjacent fished areas (spillover). Theory predicts that fished areas immediately adjacent to reserve borders should receive highest rates of spillover of juveniles and adults, such that catch rates are highest near borders (Hilborn et al. 2006). However, high effort immediately adjacent to reserves (fishing the line) may ultimately depress local abundance such that catch rates near borders are lower than sites farther from reserves (Kellner et al. 2007). Catch rates near reserve borders that are significantly higher than catch rates at sites far from reserves, or that are lower but accompanied by high effort, are often interpreted as reserve spillover effects. Such patterns have been observed for reef fishes in the Philippines (Russ et al. 2004, Abesamis and Russ 2005, Abesamis et al. 2006) and Kenya (McClanahan and Mangi 2000, Kaunda-Arara and Rose 2004), artisanal fisheries in the Mediterranean (Harmelin-Vivien et al. 2008, Forcada et al. 2009, Stobart et al. 2009), spiny lobster in the Mediterranean (Goñi et al. 2008), and a trawl fishery in the northeastern United States (Murawski et al. 2005). Tagging studies also provide important insight into movement across reserve borders (e.g., Kelly et al. 2002, Kelly and MacDiarmid 2003, Goñi et al. 2006), but such studies are less common due to high costs and logistical constraints. Marine reserves benefit conservation through increased abundance and/or size of adult target organisms inside borders, and such increases can impact fisheries through spillover that is detectable in catch and effort dynamics at reserve borders.

Potential fishery benefits of marine reserves are likely to be highly variable among fisheries (Parrish 1999, Hilborn et al. 2004) and individual reserves where habitat features are heterogeneously distributed and influence spillover (Tupper 2007, Goñi et al. 2008, Freeman et al. 2009). As a consequence, the spillover potential of a given reserve may be difficult to predict. Even where empirical evidence exists, scientists may interpret data differently and at least one high-profile study that attributes improved catches to a nearby reserve (Roberts et al. 2001) has been questioned (Hilborn 2006). Such uncertainty is a challenge for marine scientists and contributes to stakeholder skepticism regarding the development of reserves as fishery management tools, especially where spillover effects are predicted by simplistic models that do not account for uncertainty and site-specific factors (Agardy et al. 2003, Sale et al. 2005). For marine reserves to reach their potential as conservation and management tools, there is a need for monitoring and assessment strategies that foster stakeholder support and limit uncertainty in measurements of conservation and fishery effects.

One potential strategy for limiting uncertainty and fostering stakeholder support is the inclusion of fishermen in reserve monitoring and fishery research. Collaborative fisheries research (CFR), in which fishermen work with scientists in some or all phases of research, is an effective means of increasing the quality and quantity of data collected for management and policy assessments (NRC 2004). Additionally, the scientific benefits of CFR are complemented by social benefits that often include greater buy-in for management (McCay and Jentoft 1996, Conway and Pomeroy 2006, Hartley and Robertson 2009). Due to the social and scientific benefits of CFR, there are widespread calls to expand this practice (Pew 2003, U.S. Commission on Ocean Policy 2004). Collaborative fisheries research is well suited to the study of interactions between fisheries and marine reserves. Compared with traditional ecological sampling techniques (e.g., visual scuba surveys), CFR may be superior for studying spillover because catch rates at reserve borders are readily compared to fishing effort distribution, catch throughout the range of the fishery, historical catch records, and other fishery relevant data sets. Additionally, CFR can enhance assessment of conservation effects and population changes inside vs. outside of reserves because catch rates provide abundance proxies for cryptic, nocturnal, or deepwater taxa that are difficult to survey visually. The advantages of CFR for measuring both the conservation and fisheries effects of marine reserves make it a promising tool for improving assessment and stakeholder participation.

Here we report the results of a CFR program designed in part to test three research questions concerning the influence of a network of marine reserves on an actively fished marine invertebrate, the California spiny lobster (Panulirus interruptus). First, we tested whether over a relatively short period of time (six years after reserve establishment) reserves influenced trap yield (a proxy for lobster abundance) and lobster size structure in reserves using a before vs. after comparison. Second, we tested whether spillover occurred and influenced trap yield and mean lobster size immediately outside reserve borders. Finally, we tested whether commercial fishing effort near reserve borders was higher than at more distant sites,

indicating that lobster fishermen respond to reserves through fishing the line.

MATERIALS AND METHODS

Study sites

Research was conducted at Santa Cruz and Santa Rosa Islands, part of the northern Santa Barbara Channel Islands (SBCI) located ~30 km offshore in the western portion of the Southern California Bight (Fig. 1). The archipelago is a productive fishing ground for *Panulirus interruptus* and many other invertebrates and fishes that inhabit nearshore rocky reefs. The state of California designated a network of 10 no-take marine reserves and two marine conservation areas in the SBCI in April 2003. The reserves encompass 21% of state waters (high tide line to 4.8 km offshore) surrounding the SBCI, while the other 79% remains open to commercial and recreational fishing (CDFG 2008). We sampled at sites associated with three marine reserves: Scorpion, Gull (Santa Cruz Island), and Carrington (Santa Rosa Island; Fig. 1). A regional assessment of the effects of SBCI reserves on lobster catch, using a before–after control–impact paired-series (BACIPS) assessment of fishery-dependent landings data reported from the SBCI and nearby mainland, where reserves are not yet located, found that total lobster catch and revenue of fishermen that fished within the reserve network decreased in the five-year period after the reserve network was established (Guenther 2010). That BACIPS analysis also found that total catch and revenue were not declining further but were increasing in the sixth year after reserve establishment. Here we examine more localized responses in yield, lobster populations, and the response of fishermen around a subset of the reserves within the network.

Individual trapping sites inside and outside of each reserve were selected in collaboration with five commercial fishermen with a combined total of >60 years fishing at each site prior to the 2003 reserve establishment. Collaboration during site selection and other activities is beneficial because fishermen spend more time at sea than scientists and therefore have enhanced opportunity to observe and understand the biological and physical processes that influence resource dynamics. This understanding is commonly referred to as fisher knowledge or local ecological knowledge (LEK). When incorporated into ecological studies, LEK can enhance hypothesis formation, sampling efficiency, and the interpretation of results (Hartley and Robertson 2009). Accessing the LEK of fishermen allowed us to identify reefs with similar historical (i.e., pre-reserve) catch dynamics, physical/biological habitat characteristics, and was essential in guiding selection of individual trapping sites located inside (referred to in this report as In), adjacent outside (Near), and ~2–6 km farther away from (Far) reserve borders (Fig. 1). Fishermen worked with scientists to identify two to four reefs inside and outside each reserve that were similar according to the following

criteria: (1) historical trap yield; (2) historical population size structure; (3) depth and surrounding bathymetry; (4) physical habitat characteristics; and (5) weather exposure and oceanographic conditions. This information was generated through discussion, scuba surveys, and comparison of pre-reserve trap yield. We selected four trapping sites for the Scorpion reserve (two In, one Near, one Far), and five (three In, one Near, one Far) for the Gull and Carrington reserves (Fig. 1).

Effects of reserves on trap yield

We tested whether three reserves (Gull, Scorpion, Carrington) influenced the spatial patterns of trap yield in and around reserves by comparing trap yields recorded by fishermen in commercial fishing logbooks before reserves were established (1998–2002) with trap yields that we generated in a collaborative trapping program after reserves were established (2007 and 2008). A before vs. after comparison of logbook data alone was not possible because commercial fishing is prohibited in reserves. As required by law, logbook data record effort and catch as the number of traps pulled and legal lobsters retained, respectively, in catch areas defined by specific geographic landmarks selected by individual fishermen. Detailed calculations of pre-reserve trap yield are provided by Guenther (2010). Briefly, we were granted access to hard-copy logbooks through collaboration with partners in the California Department of Fish and Game (DFG) and the commercial fishery. Guenther digitized this data set as a GIS layer, conducted fisherman interviews and GIS mapping to define the spatial overlap of our research trapping areas and the trapping areas associated with fisherman-defined landmarks in logbooks, and then calculated the daily average trap yield (i.e., number of lobsters caught per trap per day) by the fishery in the immediate vicinity of our In, Near, and Far sampling sites.

We measured trap yield as well as the length of legal-sized lobsters in the After period from traps placed at In, Near, and Far sites associated with each of the three reserves (total traps = 15–20 replicate traps per In, Near, and Far site × 3 trapping sites = 45–60 traps per reserve). Traps were sampled every two to four days at each site during August–October in both 2007 and 2008. Across-site comparisons of research trap yield are based on data that were collected prior to the commercial fishing season, which begins in early October every year. We constrained analysis of trap yield data to this time period because fishery effort can influence catch rates, such that sampling amidst variable effort (i.e., high effort at Near and Far sites but low effort at In sites) might have biased our results. Data collected during periods when our sampling overlapped with the commercial fishing season were used in length frequency analyses. Traps were deployed haphazardly at 2–20 m water depth within areas stratified by reef boundaries (i.e., extent of hard bottom substrate) that were delineated prior to sampling based on qualitative scuba
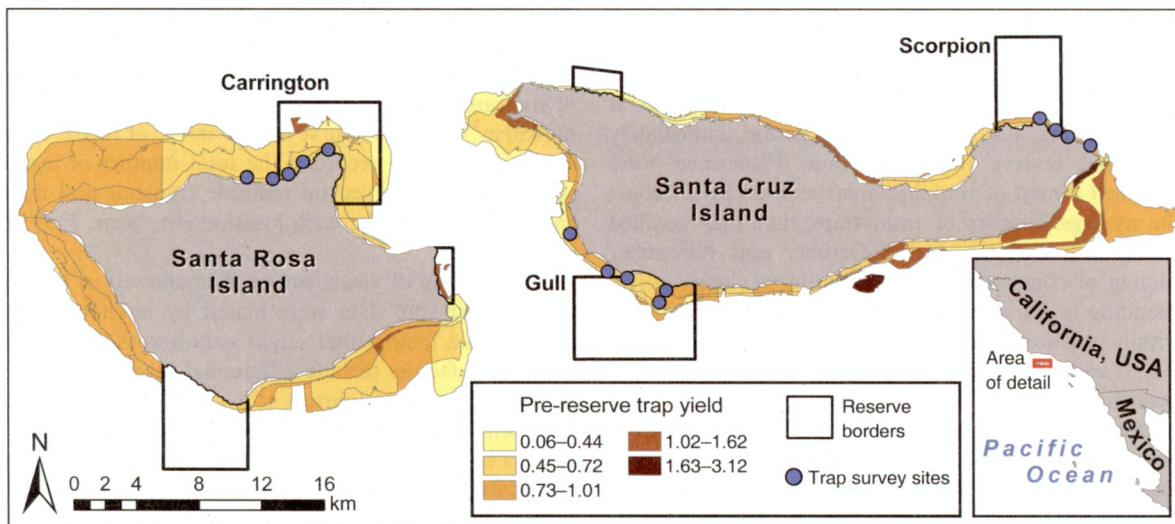
FIG. 1. Map of sites where collaborative lobster trapping surveys took place (blue circles) at Santa Cruz and Santa Rosa Islands in the Southern California Bight, USA (inset). Also shown are marine reserves (black rectangles) and polygons representing area-specific pre-reserve lobster trap yields (mean number of legal sized lobsters/trap) during the period from 1998 to 2002, as calculated from analysis of commercial lobster logbooks.

surveys, 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 priori by fishery partners as a distance that would not cause traps to compete against each other, and individual lobstermen often set their own traps much closer together. We recorded the depth, time, date, and GPS coordinates for each trap when sampling, as well as the total number, sex, carapace length (to the nearest millimeter using vernier calipers), injuries (e.g., missing legs or antennae), and reproductive condition of all lobsters in the trap. We minimized stress to lobsters on deck by shading them with wet burlap sacks, placing them in standing seawater, and returning them to the ocean as quickly as possible. Lobsters were returned to the exact location of capture (using GPS coordinates) and released by hand.

Trapping was conducted in a two-stage process consisting of a training period conducted aboard commercial vessels followed by trapping from a university boat for much of the remainder of the program. A unique aspect of our collaborative program was the transfer of LEK from fishermen to M. Kay, who received extensive training from a veteran lobsterman (C. Miller) prior to the project. During this training, Kay worked as crew during commercial lobster fishing trips in and around the study sites. Additionally, other lobstermen on the fishing grounds provided support during the project, such that the biological sampling was facilitated by a collective and community-supported LEK transfer from the fishery to the biologist. Consequently, after traps were initially deployed from commercial vessels and critical safety and fishery

information about each site had been communicated, the biologist possessed the skills to sample and re-deploy traps from a university-owned vessel retrofitted with a commercial-grade trap hauler.

Traps used in this study were identical to those used in the fishery for P. interruptus at the SBCI (91.5 × 122 × 45.7 cm tall; constructed of Riverdale 2 × 4 inch [5.1 × 10.2 cm] mesh wire; attached at their base to a single 91.5 × 122 cm rectangular frame constructed from 1 inch [2.5 cm] diameter steel rod; and coated with a hydrocarbon asphalt sealant used to prevent corrosion). The only difference between research and commercial traps is that the former did not have escape ports for sublegal adult lobsters (~70–82.5 mm). Traps were baited with ~500 g of Pacific mackerel (Scomber japonicus) that was placed in 1-L plastic bait capsules (one per trap) after each sampling event. Each trap was connected to a 3/8 inch (0.95 cm) polypropylene line and surface buoy that allowed for rapid location and retrieval as in the commercial fishery.

The validity of comparing logbook data (1998–2002) and research trapping data (2007–2008) hinges upon two assumptions: (1) research trapping was not biased (i.e., caught more or fewer lobsters per trap) relative to commercial trapping, and; (2) pre-reserve trap yield across sites inside/outside reserves did not converge upon a common value due to uneven effort across sites. To clarify the second assumption, trap yield can be a confounded measure of area-specific productivity in fisheries where effort is spatially heterogeneous and causes catch per unit effort to equilibrate across space in accord with the equal gains predictions of ideal free distribution (e.g., Swain and Wade 2003). To ensure that our pre-reserve trap yield estimates were reliable for analysis and not confounded by spatially varying effort

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trends, we measured effort levels in each research trapping area prior to reserve establishment using LEK of our fishery partners. Specifically, we interviewed fishermen to determine the density of traps present at each trapping site for the five-year period immediately preceding reserve implementation. Fishermen were provided a map of trapping areas and asked to report the average number of total traps that they recalled seeing in each area during October and November (timing of commercial season time most closely corresponding to our surveys) from 1998 to 2002. Estimates within each area were averaged from all respondents ($N = 2$–5) and were used to test for effort differences across sites (In, Near, Far) at each reserve.

During the 2007 and 2008 field seasons we conducted two activities to test the assumption that yields from research trapping and logbooks were unbiased and comparable: (1) a comparison of yields from commercial fishery trapping (estimated from logbook data) and research trapping that took place simultaneously at the Scorpion Near and Far sites, and; (2) port sampling. Port sampling consisted of meeting fishermen at the dock and measuring the size structure of lobsters harvested from relatively large regions outside of reserves that encompassed our Near and Far sites. Collection of these fishery-dependent data expanded the spatial coverage of our sampling outside reserves, and helped ensure that our trapping data were representative of commercial catches. In total, we port sampled 19 times for lobsters caught at Santa Cruz Island and 27 times for those caught at Santa Rosa Island.

Visual scuba surveys of lobster density

We compared our trap yield results inside vs. outside of reserves in the before and after time periods with lobster abundance data collected by National Park Service (NPS) scuba divers in the NPS kelp forest monitoring program. The NPS data were collected before and after reserve implementation (April 2003) from 11 sites distributed across Santa Cruz ($N = 5$ sites), Santa Rosa ($N = 3$), and Santa Barbara ($N = 3$) Islands. Three of the sites were located inside existing reserve boundaries, and two sites were located inside the Gull and Scorpion reserves on reefs where we trapped. The other eight NPS sites did not overlap with our trapping areas. To ensure temporal consistency with our trapping data, NPS data used to compare lobster densities before vs. after reserves were constrained to the 1997–2003 and 2007–2010 summer field seasons, respectively. NPS divers count lobsters at each site once per year on 12 replicate 20×3 m transects (12 transects $\times$ 60 m^2 = 640 m^2 sampled at each site) as part of a broader community-level kelp forest monitoring protocol described by Davis et al. (1997). We estimated annual mean lobster density for each site from these data.

Because NPS data provide temporal coverage but do not align spatially with our trapping areas, we also report data from our own visual scuba surveys. From August to October 2008, we conducted 80 scuba transect surveys across 13 of our 14 trapping sites inside and outside reserves. At each site, we conducted a minimum of six transect surveys on transects that were 45 m $\times$ 10 m (450 m^2). Thus, we surveyed $\geq$2700 m^2 of reef at each site in Fig. 1. We recorded the total number of legal-sized lobsters observed on replicate transects and then calculated a mean for each location (In, Near, Far) at each reserve.

The addition of visual survey data allowed us to test whether our trap data were biased by unknown trap performance factors that might vary across space and time. Such factors include differential catchability (i.e., the probability that lobsters at a given site will enter a trap) and fishing effort that was lower during scientific surveys (After) than during the Before period, when trap yield data were taken from commercial logbooks. Visual survey data also provided an additional and direct measure of lobster responses to SBCI reserves.

Tagging data to further test for spillover

Although we emphasize spatially explicit trap yield and effort patterns to detect spillover of lobsters, we also conducted a companion tag–recapture study to detect movement of lobsters across reserve borders. During trapping events at In, Near, and Far sites, all lobsters were tagged with an individually numbered T-bar tag (TBA-2 standard; Hallprint Tags, Hindmarsh Valley, Australia). Tags were applied through a thin membrane on the ventral surface between the tail and carapace, such that the "T" portion of the tag was anchored in muscle and persisted through molting. Tag–recapture studies were conducted prior to the 2007 and 2008 fishing seasons to reduce potential bias caused by commercial fishing (October to March) and the unreported capture of tagged animals.

Fishing effort around reserves

To test whether fishermen aggregated effort along reserve borders (fishing the line) we mapped the distribution of commercial effort (trap buoys) at Near and Far trapping sites at each of the three replicate reserves. Effort was mapped from a research vessel by recording the GPS coordinates of individual buoys on four dates during the 2008–2009 fishing season: 1 October (Carrington and Gull), 1 November and 3 December 2008 (Scorpion, Carrington, Gull), and 19 January 2009 (Gull and Scorpion).

Data analysis

The number of legal sized lobsters ($\geq$82.5 mm) captured in research traps at In, Near, and Far sites was compared with a two-way ANOVA in which time (before vs. after reserves) and site location (In, Near, Far) were crossed, fixed factors. Data used for the before period (1999–2003) were from logbook analysis, and data used for the after period were from collaborative research trapping (2007–2008). Logbook catch data

report the total number of legal lobsters caught from a known number of traps in a given area, and from this we calculated the average number of legal lobsters per trap. To standardize logbook and research data, our research trapping data were also averaged across all traps at an individual site for each daily sampling event. We then calculated a grand mean of trap yield from all daily fishing and sampling events at each In, Near, and Far site before and after reserve implementation, such that the standardized unit of replication in the analysis was the average trap yield for each of the In, Near, and Far sites at each reserve (total $N =$ three replicate reserves [Gull, Scorpion, Carrington] × three site locations [In, Near, Far] × two time periods [before vs. after] = 18). The grand means for each site were pooled from ≥ 13 daily sampling events conducted in the after period of 2007 and 2008. Prior to ANOVA, grand mean data were log-transformed ($\ln[Y + 1]$) to homogenize variances. After ANOVA we compared mean effects of different treatments with Tukey's hsd post hoc tests. Data gathered to test the two assumptions that we identified (comparability of commercial fishing vs. scientific survey trapping and heterogeneous effort distribution) were analyzed with separate one-way ANOVAs.

Mean size of all legal sized lobsters in traps was compared using a one-way ANOVA in which site location (In, Near, Far) was the fixed factor (total $N =$ three replicate reserves [Gull, Scorpion, Carrington] × three site locations [In, Near, Far] = 9). The carapace lengths of all legal sized (≥ 82.5 mm) lobsters trapped at a given site were averaged for each sampling day, and from these daily means we calculated grand means at each site for use in our analysis. Before vs. after comparisons were not possible in this analysis because size data are not recorded in logbooks. After ANOVA, a Tukey's hsd post hoc test was used to compare means across sites (In, Near, Far).

Length frequency data from each site location (In, Near, Far) were compared within (but not across) individual reserves using Kolmogorov-Smirnov (KS) tests. Similarly, survey trapping data at the Gull and Scorpion sites (In, Near, Far for both reserves) were then compared with port sampling data from Santa Cruz Island, and survey data from Carrington sites were compared with port sampling data from Santa Rosa Island with KS tests.

To test whether reserves influenced fishery dynamics through fishing the line, the location and density of commercial lobster trap buoys in all Near and Far sites were examined using ArcGIS 9 (ESRI 2009). Density of commercial effort in the Near vs. Far sites was compared with a one-way ANOVA using the commercial buoy data collected in 2008–2009. The distribution of traps within the Near sites was examined with linear regression, where distance from reserve border (measured at the midpoint of sequential 50-m alongshore segments) was the independent variable and the dependent variable was the number of traps in each

50-m segment. Buoy data were pooled from all surveys ($N = 3$ surveys at Carrington and Scorpion, $N = 4$ surveys at Gull) at each Near site and separate regressions were run for each Near site.

Data of lobster abundance estimated from scuba surveys were analyzed in two ways. First, a two-way ANOVA was used to test whether lobster abundance from NPS scuba surveys varied as a function of time (before vs. after; fixed factor), location (In vs. Out of reserves; fixed factor), and their interaction. Second, a one-way ANOVA was used to compare lobster abundance estimated from our own scuba surveys conducted at trapping sites during 2008 (i.e., in the after period).

For all ANOVA analyses, data were log-transformed ($\ln[Y + 1]$) to homogenize variances. Homogeneity of variance after transformation was confirmed with Cochran's test. Only data describing scientific vs. commercial trap yield in active fishing grounds (used to test assumption that research trapping was not biased relative to commercial trap yield) failed to meet standards for parametric analysis, and in those cases we report results from Welch's ANOVAs (Zar 1999). Significance level in all tests was $\alpha = 0.05$. Results tables for all ANOVAs are presented in the Appendix.

RESULTS

Trap yield, mean size, visual surveys, and movement of lobsters

Analysis of fishery logbook data from the five-year period prior to reserve implementation indicated that catch ranged from 0.59 to 0.99 legal lobsters/trap at In, Near, and Far sites. Trap yields on Santa Cruz and Santa Rosa islands in general were spatially heterogeneous and ranged from 0.06 to 3.12 legal lobsters/trap during the same period (Fig. 1). Trap yields around the three replicate reserves in the periods before and after reserve establishment varied with the interaction of time and trapping location (two-way ANOVA, time [before vs. after] × location [In, Near, Far], $F_{2,12} = 15.99$, $P < 0.001$; Fig. 2; Appendix: Table A1). A significant interaction was generated because trap yield at In sites after reserve establishment (henceforth: In-after) was significantly higher than all other time × location treatments (Tukey's, $P < 0.05$; Fig. 2), all of which were statistically indistinguishable from each other (Tukey's, $P > 0.05$). Although the mean trap yield at In-after sites was uniformly higher than all other treatments, trap yields at Scorpion In-after were about one-half the yields at Gull and Carrington In-after sites.

The number of lobsters per square meter recorded on National Park Service (NPS) scuba surveys varied with the interaction of time and location (two-way ANOVA, time [before vs. after] × site location [In, Out], $F_{1,\,117} = 14.13$, $P < 0.001$; Fig. 3A; Appendix: Table A2a). Mean lobster densities at In-after sites were 4.31–5.60 times higher than at any other time × location treatments, and the differences were statistically significant (Tukey's, $P < 0.05$; Fig. 3A). Mean lobster densities measured on
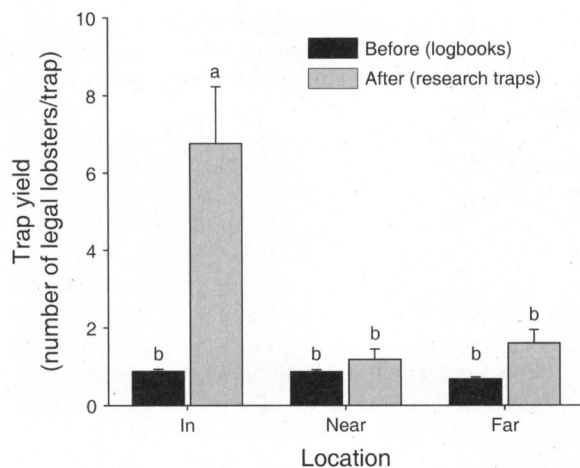
FIG. 2. Number (mean + SE) of legal sized (≥82.5 mm) lobsters caught in replicate traps at sites within (In), immediately adjacent to (Near), and 2–6 km distant from (Far) three replicate Channel Island marine reserves. Data describing conditions before and after reserve implementation are from analysis of commercial logbooks and collaborative trapping surveys, respectively. Letters represent results of Tukey's post hoc test (a > b at $P < 0.05$).

scuba transects conducted by our research team varied significantly by location (one-way ANOVA, $F_{2,6} = 10.56$, $P = 0.011$; Fig. 3B; Appendix: Table A2b). Mean lobster densities at trapping sites In reserves were 4.23 and 5.38 times higher than mean densities at our Near and Far sites, respectively, and the differences were significant (Tukey's, $P < 0.05$).

Research traps and commercial traps (reported through logbooks) that were deployed in the same area during the 2006–2007 and 2007–2008 fishing seasons did not differ in yield per trap (one-way ANOVAs: 2006–2007 Welch's $F_{1,49} = 0.007$, $P = 0.93$; 2007–2008 Welch's $F_{1,53} = 1.75$, $P = 0.19$; Appendix: Table A3), thus indicating that research trapping was not biased relative to commercial trap yield. With regard to the potential for effort heterogeneity to confound our use of trap yield as a metric for pre-reserve conditions, fisherman interviews suggest no statistically significant pre-reserve effort heterogeneity across our survey sites during the 1998–2002 fishing seasons (one-way ANOVA, $F_{2,25} = 1.43$, $P = 0.26$; Appendix: Table A4). Thus our use of logbook and research trapping data to compare trap yield before vs. after reserves is justified.

The size of legal sized lobsters caught in traps after reserve implementation varied significantly by location (one-way ANOVA, $F_{2,6} = 8.94$, $P = 0.016$; Appendix: Table A5) and was statistically greater at In sites (all three reserves = 100.4 ± 1.20 mm, mean ± SE) than at the Near or Far sites (Tukey's, $P < 0.05$), while size at Near (92.8 ± 1.85 mm) and Far (93.4 ± 0.92 mm) sites did not differ (Tukey's, $P > 0.05$). Sizes of lobsters In the Scorpion, Carrington, and Gull reserves were 102.2 ± 0.67, 100.7 ± 0.47, and 98.13 ± 0.36 mm, respectively. Outside reserves, the size of lobsters at Near and Far

sites ranged from 89.7 ± 0.60 mm (Gull Near) to 96.0 ± 0.81 mm (Carrington Near).

All of the 499 lobsters that were tagged and recaptured across In, Near, and Far sites at the three replicate reserves were recaptured nearest to the reserve where they were tagged. A total of 310 lobsters originally tagged at In sites were recaptured. Of these, 94.5% were recaptured within the In site where they were tagged, while 5.2% and 0.3% exited the reserve and were recaptured in Near and Far sites, respectively (Fig. 4). Similarly, 97% of lobsters ($N = 127$) tagged at Far sites were later recaptured at that same site, while 1.5% were recaptured at both the Near and In sites. In contrast, of the 62 lobsters tagged in Near sites, only 70% were recaptured within the same Near site, whereas 24% were recaptured at In sites and 6% were recaptured at Far sites.

The size structure of lobster populations at all three reserves had a greater proportion of large lobsters In reserves than at Near or Far sites (Fig. 5; Kolmogorov-Smirnov [KS], $P < 0.05$). There was no difference in size structure between Near and Far sites for both Scorpion (KS, $P = 0.13$) and Gull (KS, $P = 0.18$) reserves, but size structure was significantly different at Carrington Near and Far sites (KS, $P < 0.05$). Size frequency data from
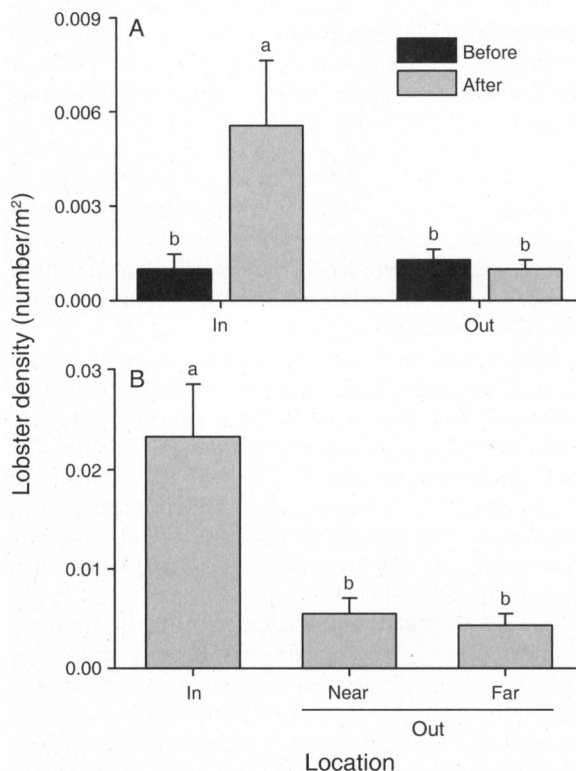

FIG. 3. The density of lobsters (mean + SE) observed on visual scuba surveys conducted by (A) the National Park Service (NPS) kelp forest monitoring program and (B) our research team. NPS data include all sizes of lobsters observed, while data from our research team include only legal sized lobsters. Letters represent results of Tukey's post hoc test (a > b at $P < 0.05$).

port sampling (fishery dependent and collected in the after period) showed similar patterns to data from trap surveys at Near and Far sites (Fig. 5). However, port sampling data from Santa Cruz and Santa Rosa Islands had significantly more large lobsters than our scientific trap sampling when we pooled Near and Far data at all three reserves (KS, $P < 0.001$). Such results were not surprising because the port sampling data set consisted of an order of magnitude more lobsters than the trap sampling data.

Commercial effort distribution

We mapped the location of 617 total buoys at all Near and Far sites on four dates during the 2008–2009 fishing season. Trap densities within these sites were not statistically different (one-way ANOVA, $F_{1,18} = 1.61$, $P = 0.22$; Appendix: Table A6). Traps were generally distributed alongshore, although the total number and position changed with time, and we did not observe a concentration of commercial traps near reserve borders (Fig. 6). At Scorpion and Carrington reserves, traps were consistently absent immediately adjacent reserves, and regression analysis revealed no relationship between distance from reserve border (predictor) and the number of traps (response) within any of our three Near sites ($P > 0.05$ for all tests). Qualitative comparison of pre-reserve effort (fishermen interviews) and post-reserve effort (buoy surveys) indicates that effort at each site has not drastically shifted since reserve implementation (Fig. 6, insets).

DISCUSSION

The number and mean size of legal (≥ 82.5 mm) lobsters captured inside reserves were greater than in traps placed outside in fished areas, and we therefore conclude that Santa Barbara Channel Island (SBCI) reserves have significant conservation benefits for spiny lobster. These benefits developed within 5–6 years of reserve establishment, and included larger mean size, shifts in population structures toward larger size classes, and approximately four to eight times greater trap yield (lobster/trap) inside than outside of reserves. Similarly rapid responses to reserve protection have been observed across many taxa (Halpern and Warner 2002) and have been reported for other spiny lobster species (MacDiarmid and Breen 1993, Goñi et al. 2001, Follesa et al. 2008, Pande et al. 2008). Parnell et al. (2005) used fishery-independent historical data from scuba surveys to examine temporal changes in the density of *P. interruptus* at sites inside a southern California reserve, and they observed an eightfold decrease from 1979 to 2002 (reserve implemented in 1971). However, surveys conducted in 2002 reported by Parnell et al. (2005) did not reveal significantly higher densities of legal size *P. interruptus* inside vs. outside the same reserve. This disparity in temporal vs. spatial differences may be explained by a temporal decline in lobster abundance, both inside and outside the reserve, that reflects an overall decrease in reef productivity in the region (Dayton et al.
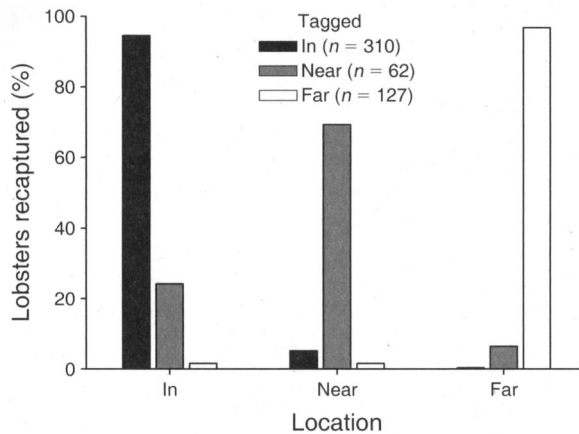

FIG. 4. The percentage of lobsters that were tagged, and subsequently recaptured, in each of the three survey locations (In, Near, Far). Data for each survey location are pooled from all three reserves. The legend indicates original tagging locations and the number of lobsters recaptured from each tagging location (not the total number tagged in each location). Data are from lobsters tagged and recaptured during research trapping surveys prior to the 2007–2008 and 2008–2009 fishing seasons.

1998). Understanding the ecological effects and fisheries management potential of marine reserves against the backdrop of sliding baselines further underscores the need to collect robust spatiotemporal data.

The trap yield increases that we observed across time (before vs. after) at sites In reserves may have been partially due to the fact that effort was lower during our research surveys (after) than during fishing seasons from which logbook data were estimated in the before period. However, it is unlikely that this effort difference is primarily responsible for the large increases inside reserves: if this were the case, then similar increases at the Near and Far sites would have been observed. Furthermore, the magnitude of trap yield increases inside reserves is remarkably similar to increases observed in the two independent scuba surveys (NPS data and our own surveys). Although mean lobster densities from our scuba surveys were approximately five times greater than those from NPS surveys, relative increases inside vs. outside were nearly identical (Fig. 3). Our density estimates may have been higher than those of NPS because we worked in stratified areas of high lobster abundance and/or because our transects were both larger (very few with zero lobsters) and focused explicitly on lobster counts. The disproportionately large increase in trap yield inside vs. outside reserves, and the consistency between trap and scuba survey data, strengthens our conclusion that the observed trap yields inside reserves were indeed population level reserve effects and not an artifact of confounded trap performance due to spatiotemporal differences in fishing effort or catchability. The extent to which differential effort in the before vs. after periods might have influenced trap yield is illustrated by the yield differences across time at
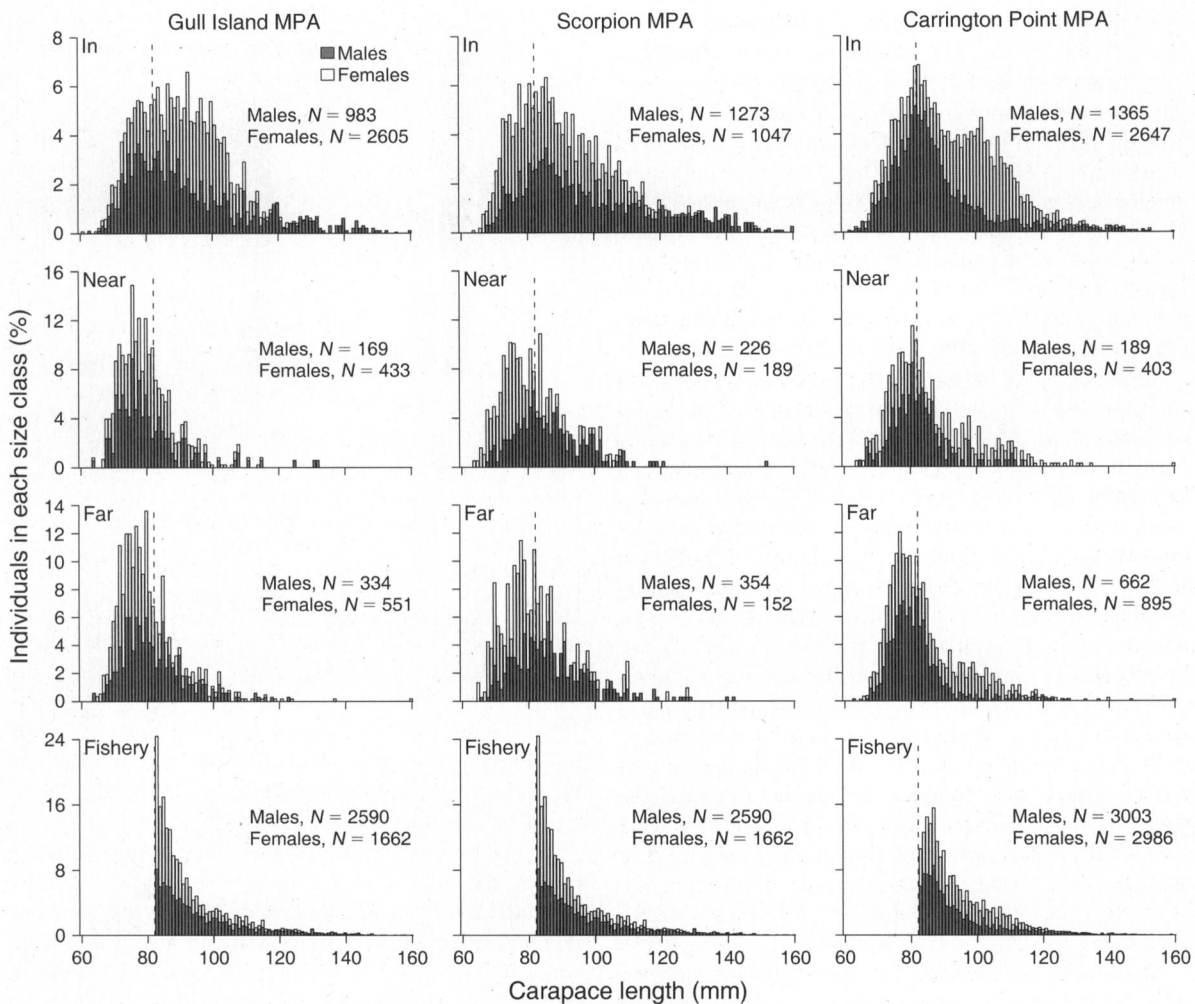
FIG. 5. Length frequency histograms for lobsters caught during collaborative trapping surveys and concurrent port sampling of commercial catch from Santa Cruz and Santa Rosa Islands. Fishery data for the Scorpion and Gull reserves are identical because port sampling was conducted for the entirety of Santa Cruz Island, but catches were not segregated at a finer resolution.

the replicate Near and Far sites (Fig. 2), but other temporally dynamic factors might also contribute to these differences.

Although many studies document spiny lobster population increases inside marine reserves, relatively few report aggregate data collected across replicate reserves (but see Edgar and Barrett 1997, 1999, Kelly et al. 2000, Mayfield et al. 2005), and to our knowledge only two include data prior to reserve implementation (Shears et al. 2006, Follesa et al. 2008). We know of no study that has combined before vs. after data across replicate reserves, even though spatiotemporal variability is an important consideration when measuring reserve effects. Spatial variability in lobster abundance and population structure inside reserves has obvious pertinence for conservation and biodiversity protection, but such patterns also have important implications for fisheries. Specifically, the potential for reserves to increase fisheries yield through export of larvae is dependent upon increased lifetime egg production of

populations inside reserves (Guénette et al. 1998, Botsford et al. 2009). However, reproductive output and lifetime egg production from reserves is influenced by the abundance and population structure of target organisms (Tetreault and Ambrose 2007, Taylor and McIlwain 2010), which we found to vary across reserves in this study (Fig. 5). Additionally, there is growing interest in use of marine reserve populations as proxies for unfished stocks in fishery assessments (e.g., Morgan et al. 2000, Willis and Millar 2005, Wilson et al. 2010). Our results imply that spatial variation in population size structure and trap yield should be considered and measured when selecting reserve sites as ecological and fishery baselines.

We did not observe higher trap yield or effort at sites Near vs. Far from reserve borders, and therefore conclude that spillover did not significantly influence trap yield or effort distribution outside reserves. A similar result indicating that reserves did not enhance trap yield outside reserves was estimated by Guenther (2010) at a

geographic scale of the whole reserve network using logbook data only. The absence of catch and effort patterns indicative of spillover is corroborated by tag–recapture data (Fig. 4) and can be explained by several factors. The most likely explanation is that the SBCI reserves were established only six years prior to our study, and had not yet experienced population biomass increases sufficient enough to cause resource limitations that initiate density-dependent emigration (e.g., Sánchez-Lizaso et al. 2000, Shears et al. 2006). This hypothesis is supported by recent work suggesting that, unlike rapid population increases observed for fished organisms inside reserves, indirect effects such as density-dependent spillover typically develop over decadal time scales (Babcock et al. 2010). Additionally, lobster habitat at Near sites has lower topographic relief and is structurally less complex than habitat at In sites (M. Kay, *unpublished data*), which might restrict spillover for reserve populations that are not critically resource limited. Finally, the spillover of lobster from reserves is enhanced by contiguous reef habitat that connects areas within reserves to those located outside (Freeman et al. 2009). Fishing the line for *P. interruptus* that was first observed by Parnell et al. (2006) at an older (established 1971) reserve in La Jolla, California, developed and intensified in the latter stages of the 2007–2008 fishing season and was associated with complex habitat features near the reserve boundary (Parnell et al. 2010). We observed no such spatial configuration of reefs at the SBCI reserve network, at least for habitat considered exceptionally productive for lobster fishing. In fact, most reserve borders in the SBCI network were placed in sandy areas or at considerable distance from historically productive reefs inside reserves. Consequently, the absence of evidence for spillover and/or fishing the line is not surprising, especially for such young reserves.

Another possible explanation for the absence of spillover-driven catch and effort patterns, which may interact with the time and habitat factors described previously, is a moderate exploitation rate for lobster outside reserves. Spillover effects such as increased yield and effort near borders are most pronounced for fisheries in which populations outside reserves are heavily exploited (e.g., Goñi et al. 2010). In such fisheries, very high total mortality rates are detectable in length frequency data when the data are truncated and contain relatively few legal sized (or larger) lobsters (e.g., Edgar and Barrett 1999, Iacchei et al. 2005, Barrett et al. 2009, Goñi et al. 2010). Our port sampling data (Fig. 5) do not indicate such extreme truncation and suggest that exploitation at the Channel Islands may be lower than in other spiny lobster fishing grounds, even within California (Iacchei et al. 2005). Beverton and Holt (1956) established a formal relationship between total mortality, growth rates, and catch data that estimates total mortality (Z; natural mortality + fishing mortality) as a function of length frequency data and the von Bertalanffy growth parameters k and L_∞ (see also
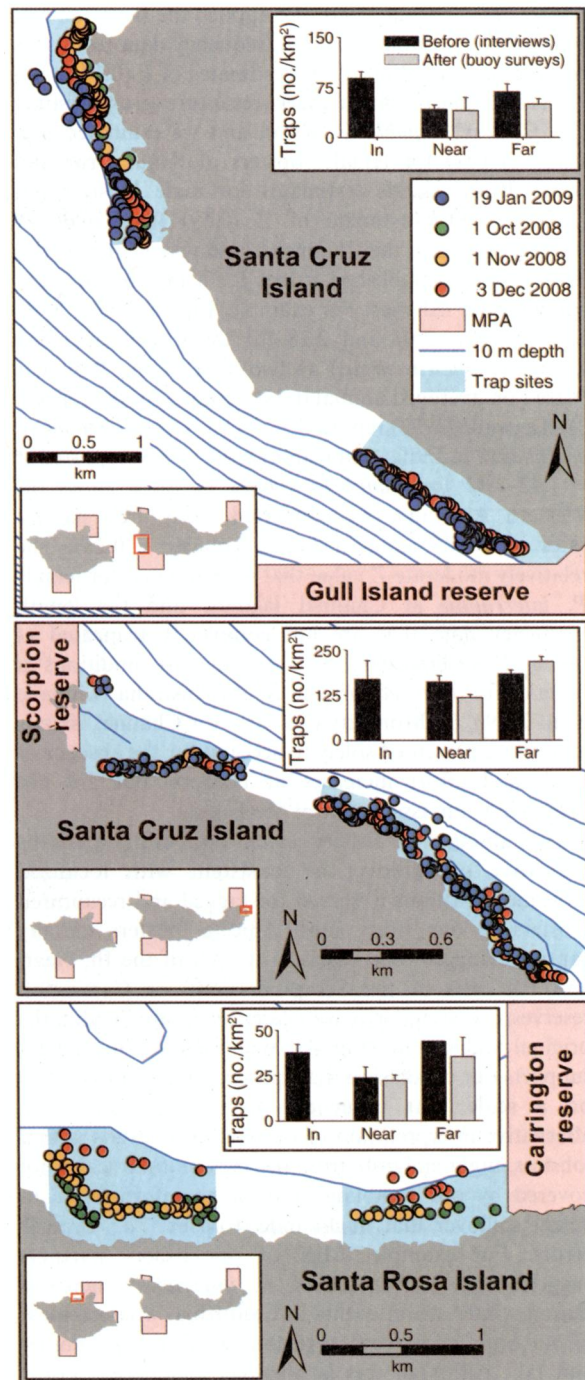

Fig. 6. Commercial effort (buoy) distribution at each reserve site on four (Gull) or three (Scorpion, Carrington) dates during the 2008–2009 fishing season. Blue polygons are areas where collaborative trapping took place. Commercial effort was not sampled between the Near and Far polygons (sites), but was qualitatively similar. Insets show effort patterns (mean + SE) before and after reserve implementation, as measured from fisherman interviews and buoy surveys, respectively. MPA is the marine protected area.

Sparre and Venema 1998). We applied the Beverton and Holt (1956) formula to length frequency data from sites outside reserves (Fig. 5) and estimates of k (0.105) and L_∞ (121.5 mm) from a mark–recapture growth study (M. C. Kay, *unpublished data*), and we estimated a Z value of 0.59 for female lobsters at Santa Cruz and Santa Rosa Islands (estimates for male lobsters not available). Our estimate of Z (0.59) for female *P. interruptus* within the Channel Island reserve network is low relative to published values for a number of other spiny lobster fisheries. For example, Lipcius et al. (2001) reported $Z = 2.01$ and 2.28 for the Caribbean spiny lobster (*Panulirus argus*) at two sites in the Bahamas (based on averaged annual data presented in their Table 3); Kagwade (1993) reported $Z = 0.93$–1.24 for *Panulirus polyphagus* in India; and Caputi et al. (2008) reported $Z = 1.42$–2.12 for *Panulirus cygnus* in three zones off Western Australia (we converted from their harvest rates of 70–85% and natural mortality $= 0.22$). The relatively moderate Z value that we estimated for female *P. interruptus* at Channel Islands, and the length frequency data that are not completely truncated at the legal size limit (Fig. 5), are similar to conditions in fisheries for *Jasus edwarsii* in South Australia (Linnane et al. 2009a, b). Mortality estimates for Channel Islands lobster are presented solely to account for the absence of catch and effort increases at borders, but are not intended as an assessment of the fishery.

The absence of fishery catch and effort patterns indicative of spillover is consistent with localized movement patterns observed for tagged and recaptured lobsters at our study sites. Among lobsters initially captured, tagged, and released at each of the In, Near, and Far sites at the Scorpion, Gull, or Carrington reserves, a vast majority were later recaptured within the original tagging site (Fig. 4). Such localized movement supports our conclusion that spillover was not operative on a scale that influenced fishery dynamics. An alternative interpretation of our spillover results is that lobsters might emigrate from reserves on time scales not covered by our sampling, and we therefore failed to detect spillover that might indeed occur (i.e., Type II error). For example, LEK of our fishery partners suggests that movement of *P. interruptus* increases during winter storm events in California, whereas most of our trapping surveys were conducted in late summer and fall. Although this is possible, commercial effort surveys were conducted later in the season and showed no indication of fishing the line. Furthermore, we explicitly tested the predictions of spillover as a process driven by nonseasonal movement due to density dependence (Polacheck 1990, DeMartini 1993, Sánchez-Lizaso et al. 2000), diffusion (Hilborn et al. 2006, Kellner et al. 2007, Walters et al. 2007), or home ranges that cross reserve borders (Moffitt et al. 2009). Exploration of temporally dynamic (e.g., seasonal, ontogenetic) emigration from reserves is newly developing (Botsford et al. 2009). Expanded tagging or sampling

for abundance gradients inside reserves are possible approaches for studying spillover not detectable with fishery-dependent techniques alone, and merging fishery-dependent and fishery-independent approaches represents an important frontier for CFR.

Our study is a valuable contribution to studies of reserve–fishing interactions because we demonstrate the potential for CFR to improve ecological assessments that inform policy. Fishery-dependent methods and metrics enhanced this study by allowing us to perform a before vs. after analysis, accurately and precisely measure trapped lobsters to the nearest 1 mm (not feasible with diving methods), reliably compare effort and catch patterns near borders, perform a tag–recapture study, access fishermen LEK, compare results with port sampling data, and estimate total mortality (Z) for fished areas. Additionally, we established community-based capacity for monitoring future changes to this coupled human–natural system and the broader fishery. Our collaborative approach not only improved the ecological assessment, but our ecological findings feedback into the human component of the system. For example, fishery partners in this study view the work as useful because it has increased their awareness and trust for science-based management. As a consequence, the California Lobster and Trap Fishermen's Association supports continued research at SBCI, as well as expansion of our collaborative approach throughout the U.S. range of the *P. interruptus* fishery, in an effort to engage its members in stakeholder-based reserve monitoring, data collection for stock assessment, and a third-party sustainability certification. This is a direct impact of our innovative partnership at SBCI and exemplifies the stewardship that often arises from collaborative resource management (Gutiérrez et al. 2011).

Continued spiny lobster CFR at SBCI marine reserves is important because neither the fishery nor lobster populations inside reserves are likely to be at equilibrium. In particular, LEK of senior fishermen at Channel Islands suggests that recently increased effort is likely to intensify as ex-vessel prices for California spiny lobster trend upward (from ~$9 to $17 (US$) per pound from the 2006–2007 to 2010–2011 seasons) and effort is concentrated as fishermen along the California mainland are displaced by an imminent network of marine reserves. With regard to temporal changes in lobster populations, research from older reserves in New Zealand suggests that lobster biomass will continue to increase in Channel Island reserves (Kelly et al. 2000, Shears et al. 2006), and this increase may enhance spillover. Due to this temporal dynamism, future monitoring at Channel Islands should address lobster population changes inside and outside reserves, spatially explicit catch rates, effort distribution, and fishery–reserve interactions, and a CFR approach such as we present here is an important tool. CFR has the potential to enhance many aspects of fisheries research and enable

the adaptive management of California's nearshore fisheries. This is certainly true for spiny lobster, for which the California Department of Fish and Game is developing a stock assessment and an adaptive management plan. The ability to gather information and manage adaptively will be critical as we reach (or surpass) sustainable yields for most fisheries (Hilborn et al. 2003, Mullon et al. 2005).

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SUPPLEMENTAL MATERIAL

Appendix

ANOVA tables describing effects of reserves on lobster trap yield, size, and density on the seafloor, comparisons of research vs. fishing trap yields, and effort distributions before and after reserves (*Ecological Archives* A022-020-A1).