Title

Community Based Fisheries Research on California Spiny Lobster (Panulirus interruptus) at the Santa Barbara Channel Islands

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Community Based Fisheries Research on California Spiny Lobster (*Panulirus interruptus*) at the Santa Barbara Channel Islands

A Dissertation submitted in partial satisfaction of the
requirements for the degree of Doctor of Philosophy
in Environmental Science and Management

by

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December 2011

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PUBLICATIONS

Kay MC, Lenihan HS, Kotchen M, and Miller CJ. *In review.* Habitat and distance from reserve borders influence California spiny lobster (*Panulirus interruptus*) trap performance at the Santa Barbara Channel Islands. Marine Ecology Progress Series.

Kay MC, and Wilson JR. *In press*. Spatially explicit mortality of California spiny lobster (*Panulirus interruptus*) across a marine reserve network. Environmental Conservation.

Kay MC, Lenihan HS, Guenther C, Wilson JR, Shrout SW, and Miller CJ. *In press.* Collaborative assessment of California spiny lobster (*Panulirus interruptus*) population and fishery responses to a marine reserve network. Ecological Applications.

Beck MW, Brumbaugh RD, Airoldi L, Carranza A, Coen LD, Crawford C, Defeo O, Edgar GJ, Hancock B, Kay M, Lenihan H, Luckenbach MW, Toropova CL, and Zhang G. 2011. Oyster reefs at risk globally and recommendations for conservation, restoration, and management. Bioscience 61:107-116.

Kay MC, Lenihan HS, Wilson JW and Miller CJ. 2010. The cost of vessel insurance in collaborative fisheries research: Strategies and perspectives from a program in California, USA. California Fish and Game Scientific Journal 96:33-49.

Kay MC, Lenihan HS, Miller CJ, and Barsky K. 2008. Numbers, body sizes and movement of lobster. In: Airame S, Ugoretz J (Eds.) Channel Islands Marine Protected Areas: First 5 Years of Monitoring. Santa Barbara: California Department of Fish and Game. p. 8-9.

Ruesink JL, Lenihan HS, Trimble AC, Hieman AC, Micheli F, Byers JE, and Kay MC. 2006. Introduction on non-native oysters: Ecosystem effects and restoration implications. Annual Review of Ecology, Evolution, and Systematics 36: 643-689.

Lotze HK, Lenihan HS, Bourque BJ, Bradbury R, Cooke RG, Kay MC, Kidwell S, Kirby MX, Peterson CH, and Jackson JBC. 2006. Depletion, degradation, and recovery of estuaries and coastal seas worldwide. Science 312: 1806-1809.

Kay MC, and Emlet RB. 2002. Laboratory spawning, larval development, and metamorphosis of the limpets *Lottia digitalis* and *Lottia asmi* (Patellogastropoda: Lottiidae). Invertebrate Biology 121: 11-24.

Kay MC, 2002. Recruitment in the intertidal limpet *Lottia digitalis* (Patellogastropoda: Lottidae) may be driven by settlement cues associated with adult habitat. Marine Biology 141: 467-477.

PRESENTATIONS

Kay MC, Lenihan HS, Kotchen M, and Miller CJ. 2010. Fishing, habitat, and distance from marine borders influence spiny lobster abundance on reefs at the Santa Barbara Channel Islands. Western Society of Naturalists. San Diego, California. November 2010.

Kay MC, 2010. Landscapes, Seascapes, and Stakeholders. UCSB Bren School public event. Santa Barbara, California. October, 2010.

Kay MC and Lenihan HS. 2009 Spiny lobster research at the northern Santa Barbara Channel Islands. California Department of Fish and Game spiny lobster stock assessment workshop. Santa Barbara, California. December 2009.

Kay MC. 2009. Research for sustainable fisheries: Ecology, economics, and biology. Presentation to the UC Santa Barbara Alumni Association Board of Directors. Santa Barbara, California. October 2009.

Kay MC, Lenihan HS, Miller CJ and Barsky K. 2008. Collaboration and conservation:
Monitoring impacts of Channel Islands MPA's on CA spiny lobster. Society of Conservation Biology Annual Meeting. Chattanooga, Tennessee. July, 2008.

Kay MC, Lenihan HS, Miller CJ and Barsky K. 2008. Influence of Channel Islands Marine Reserves on Spiny Lobster. Channel Islands Symposium, Special Session: The First Five Years of Monitoring the Channel Islands Marine Protected Area Network. Oxnard, California. February 2008.

Kay MC and Lotze HK. 2007. Reconstructing human-induced changes in marine ecosystems. Ecological Society of America (ESA) annual meeting, San Jose, California August 2007.

Kay MC, 2000. Laboratory settlement of the ribbed limpet, *Lottia digitalis*, onto field-collected substrata. Oral Presentation at "Larval 2000", a larval biology conference held on the campus of the University of California at Santa Cruz, June 2000.

Abstract

Community Based Fisheries Research on California Spiny Lobster

(*Panulirus interruptus*) at the Santa Barbara Channel Islands

by

Matthew C. Kay

This dissertation describes collaborative fisheries research (CFR) on California spiny lobster (*Panulirus interruptus*) at the Santa Barbara Channel Islands (SBCI). The research goals addressed in this work include: (1) establishing a collaborative approach to gathering fisheries data for assessments and management; (2) assessment of marine reserves at SBCI; (3) estimating mortality rates of lobsters populations throughout the SBCI marine reserve network; and (4) construction of fisheries models that provide context for interpreting mortality rates I estimated.

CFR enhanced assessment of marine reserves established in 2003 at the SBCI in terms of their impact in *P. interruptus* population structure and fishery interactions. After six years of reserve protection, there was a four to eight-fold 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 versus outside of three replicate reserves. Patterns in trap data were corroborated by visual SCUBA surveys that indicated a four to six-fold increases in lobster density inside reserves. These results indicate that marine reserves have strong conservation benefits for *P. interruptus*. Inside reserves, trap performance (the number and mean size of legal-sized lobsters caught in traps) was significantly influenced by proximity to reserve borders, a pattern that suggests net emigration of lobster from inside reserves to adjacent fished areas (*spillover*). Interestingly, spillover was not apparent in trap yields or commercial fishery effort distribution outside reserves, nor was it apparent in tagging studies. This suggests that spillover from reserves may have little influence of fishery yield outside reserves. However, yield due to spillover might increase as the reserves age and lobster biomass continues to increase inside reserves.

Mean total mortality (*Z*) of female lobsters was lower at sites inside reserves ($Z = 0.21$ [±0.07 SE]) than at sites outside reserves ($Z = 0.59$ [±0.02 SE]). Mean mortality at all sites inside reserves, and among sites near reserve centers (where $Z = 0.17$ [±0.05 SE]), was similar to estimates of natural mortality for other temperate spiny lobster species. Among sites inside reserves, there was a positive relationship between mortality and proximity to reserve borders, but this relationship was absent among sites outside reserves. Mortality estimates were much more variable among sites inside reserves than at sites in fished areas. Results of YPR models suggest that increased effort in this fishery will not result in commensurate increases in yield. However, current spawning potential at SBCI is ~20% (of virgin conditions), and this could decrease with increased effort. Our collaborative framework provides a stable and inclusive framework for conducting future research that informs management of this fishery and fosters stakeholder support.

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GENERAL INTRODUCTION

Community Based Fisheries Research on California Spiny Lobster (*Panulirus interruptus*) at the Santa Barbara Channel Islands

The completion of this dissertation coincides with a sobering milestone in human history. At some point during the preparation, approval, or binding of this, yet another graduate student tome, a baby will be born that will surge human population beyond 7 billion individuals. The implications of human population growth for ecology are clear. Ecology may have once upon a time been a discipline that could afford the luxury of ignoring the role of humans in natural systems, such that ecologists could make important contributions to the field through isolated study of their organisms. Those good old days are gone, or at the very least they are fading fast. Even the most ardent Pollyanna must now acknowledge that human activity impacts natural systems at every corner of the globe. A fundamental challenge for contemporary ecologists who strive for relevance in the 21st century is to understand how natural systems respond to and support human activities.

One way that humans impact marine ecosystems, and that the same ecosystems provide sustenance to humans, is through fishing. The removal of marine organisms through fishing is important for humans because it provides food, revenue, and cultural value to coastal communities. A number of recent and high profile reports suggest that fishing can have dire impacts on marine species and ecosystems (Pauly et al. 1998, Jackson et al. 2001, Lotze et al. 2006). These reports underscore the importance of understanding human impacts on marine ecosystems, and defining the capacity of these systems to provide ecosystem services such as protein, revenue, and cultural heritage attained through fishing.

In this dissertation I examine interactions of humans and California spiny lobster (*Panulirus interruptus*) in a fishery that occurs in marine ecosystems at the Santa Barbara Channel Islands (SBCI). This work is unique in part because the fishermen in this study are not subjects, but rather they are collaborative partners in the research. Their participation facilitated and enhanced the research conducted, and corroborates previously indentified advantages of collaborative research, which includes improved data quality (NRC 2004) and social benefits such as support for science and management (McCay and Jentoft 1996, Conway and Pomeroy 2006, Hartley and Robertson 2009). Improved understanding of human impacts to marine ecosystems and populations is critical because it is a first step towards ensuring sustainability of ecosystem services such as food and revenue.

This dissertation is divided in to four chapters. In chapter one, I work with commercial fishermen to measure how a network of marine reserves at the SBCI influences lobster populations and fishery dynamics. In chapter two, I expand upon chapter one and provide a spatially explicit analysis of how lobster abundance and size is influenced as a function of distance from reserve borders and due to physical habitat features on the seafloor.

In chapter three, I measure mortality rates of lobsters on reefs inside and outside SBCI reserves. This analysis employed growth data from a tag-recapture study (reported in chapter four) that accompanied the SBCI reserve assessments of chapters one and two. Estimating mortality rates inside and outside reserves allowed me to estimate mortality rates due to fishing at the SBCI. In chapter four, I construct traditional fishery models for yield per recruit (YPR) and the spawning potential ratio (SPR) of lobster populations exposed to a continuum of fishing mortality. The fishing mortality estimated in chapters three and four for lobster populations at the Santa Barbara Channel Islands are viewed in the context of these YPR and SPR models. The SPR and YPR models employ life history data that were measured as part of our collaboration or gathered from previously published accounts.

The exact estimates of mortality that I derived, and the dimensions of my YPR and SPR models, will be improved with future study and refinement of life history parameters that the models employ. The broader value of this work lies in the holistic, collaborative approach that delivers four important elements: (1) a methodology for assessment of population and fishery effects of marine reserves on California spiny lobster (chapters one and two); (2) a community based approach to gather essential data for resource assessments; (3) a spatially explicit, low cost, and data poor model for measuring harvest rates to a spatially complex and small scale fishery; (4) a model and collaborative platform for future research and management that fosters fisheries sustainability as human population continues to expand and exert increased pressure on marine resources.

LITERATURE CITED

Conway, F., and C. Pomeroy. 2006. Evaluating the human - as well as the biological – objectives of cooperative fisheries research. Fisheries 31:447-454.

Hartley, T., and R. Robertson. 2009. Stakeholder collaboration in fisheries research: integrating knowledge among fishing leaders and science partners in northern New England. Society & Natural Resources 22:42-55.

Jackson, J., M. Kirby, W. Berger, K. Bjorndal, L. Botsford, B. Bourque, R. Bradbury, R. Cooke, J. Erlandson, J. Estes, T. Hughes, S. Kidwell, C. Lange, H. Lenihan, J. Pandolfi, C. Peterson, R. Steneck, M. Tegner, and R. Warner. 2001. Historical overfishing and the recent collapse of coastal ecosystems. Science 293:629-637.

Lotze, H., H. Lenihan, B. Bourque, R. Bradbury, R. Cooke, M. Kay, S. Kidwell, M. Kirby, C. Peterson, and J. Jackson. 2006. Depletion, degradation, and recovery potential of estuaries and coastal seas. Science 312:1806-1809.

McCay, J., and S. Jentoft. 1996. From the bottom up: participatory issues in fisheries management. Society & Natural Resources 9:237-250.

NRC (National Research Council). 2004. Cooperative Research in the National Marine Fisheries Service. National Academies Press, Washington DC.

Pauly, D., V. Christensen, J. Dalsgaard, R. Froese, and F. Torres. 1998. Fishing down marine food webs. Science 279:860-863.

CHAPTER 1

Collaborative Assessment of California Spiny Lobster Population and Fishery Responses to a Marine Reserve Network

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 socio-economics (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 understandable since 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 spatio-temporal 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, MacDiarmid and Breen 1993, Acosta 2001, Lipcius et al. 2001, Mari et al. 2002, Mayfield et al. 2005), and they provide a cautionary example regarding the generality of reserve effects and the need for spatio-temporal 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 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 2008, Forcada et al. 2009, Stobart et al. 2009), spiny lobster in the Mediterranean (Goñi et al. 2008), and a trawl fishery in northeastern USA (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, US 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 datasets. Additionally, CFR can enhance assessment of conservation effects and population changes inside versus 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 I 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, I 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 versus after comparison. Second, I tested whether spillover occurred and influenced trap yield and mean lobster size immediately outside reserve borders. Finally, I 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 ten 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). I 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 I 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 me 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 (details provided below). I 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

I 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 I generated in a collaborative trapping program after reserves were established (2007 and 2008). A before versus 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, Guenther was granted access to hardcopy logbooks through collaboration with partners in the California Department of Fish and Game (DFG) and the commercial fishery. Guenther digitized this dataset 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 trap^{-1} day^{-1}) by the fishery in the immediate vicinity of our *In*, *Near*, and *Far* sampling sites.

I 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 x 3 trapping sites = 45-60 traps per reserve). Traps were sampled every two-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. I 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 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 non-independence 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. I 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 mm using vernier calipers), injuries (e.g., missing legs or antennae), and reproductive condition of all lobsters in the trap. I 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 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 x 122 x 45.7 cm tall; constructed of Riverdale® 2 x 4 inch [5.1 x 10.2 cm] mesh wire; attached at their base to a single 91.5 x 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 grams 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 trends, I measured effort levels in each research trapping area prior to reserve establishment using LEK of our fishery partners. Specifically, I 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 1998-2002. 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 I 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, I 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

I compared our trap yield results inside versus 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 I 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 versus 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 m x 3 m transects (12 transects x 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). I 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, I also report data from our own visual SCUBA surveys. From August-October 2008, I conducted 80 SCUBA transect surveys across 13 of our 14 trapping sites inside and outside reserves. At each site, I conducted a minimum of 6 transect surveys on transects that were 45 m x 10 m (450 m^2 x 6 transects per site = $\geq$ 2700 m^2 of reef surveyed at each site in Fig. 1). I 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 me to for a 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 I emphasize spatially explicit trap yield and effort patterns to detect spillover of lobsters, I 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, 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*) I 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 2008-09 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 (≥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 I calculated the average number of legal lobsters trap^{-1}. 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. I 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] x three site locations [*In*, *Near*, *Far*] x 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 I compared mean effects of different treatments with Tukey HSD *post-hoc* tests. Data gathered to test the two assumptions that I identified (comparability of commercial fishing versus 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] x 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 I calculated grand means at each site for use in our analysis. Before versus 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 was examined using ArcGIS 9 (ESRI 2009). Density of commercial effort in the *Near* versus *Far* sites was compared with a one-way ANOVA using the commercial buoy data collected in 2008-09. The distribution of traps within the *Near* sites was examined with linear regression, where distance from MPA border (measured at the midpoint of sequential 50 m along-shore 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 versus 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 I report results from Welch's ANOVAs (Zar 1999). Significance levels in all tests was $\alpha = 0.05$. Results tables for all ANOVAs are presented in Appendix A.

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 0.59-0.99 legal lobsters trap^{-1} at *In*, *Near*, and *Far* sites. Trap yields on Santa Cruz and Santa Rosa islands in general were spatially heterogeneous and ranged from 0.06-3.12 legal lobsters trap^{-1} 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*] x location [*In, Near, Far*]; $F_{2,12} = 15.99$; $P < 0.001$; Fig. 2, Table A1). A significant interaction was generated because trap yield at *In* sites after reserve establishment (henceforth: *In-After*) was significantly higher the all other time x 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 m^{-2} recorded on National Park Service (NPS) SCUBA surveys varied with the interaction of time and location (two-way ANOVA; time [*Before* vs. *After*] x site location [*In, Out*]; $F_{1,117} = 14.13$; $P < 0.001$; Fig. 3A, Table A2a). Mean lobster densities at *In-After* sites were 4.31-5.60 times higher than at any other time x location treatments, and the differences were statistically significant (Tukey's; $P < 0.05$; Fig. 3A). Mean lobster densities measured on SCUBA transects conducted by our research team varied significantly by location (one-way ANOVA, $F_{2,6} = 10.56$, $P = 0.011$; Fig. 3B, 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 2006-07 and 2007-08 fishing seasons did not differ in yield per trap (one-way ANOVAs: 2006-07 Welch's $F_{1,\,49} = 0.007$, $P = 0.93$; 2007-08 Welch's $F_{1,53} = 1.75$, $P = 0.19$, 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, $F_{2,25} = 1.43$, $P = 0.26$, Table A4). Thus our use of logbook and research trapping data to compare trap yield before versus after reserves is justified.

The mean size of legal sized lobsters caught in traps after reserve implementation varied significantly by location (one-way ANOVA, $F_{2,6} = 8.94$, $P = 0.016$; Table A5) and was statistically greater at *In* sites (mean for all three reserves = 100.4 mm ±1.20 SE) than at the *Near* or *Far* sites (Tukey's; $P < 0.05$), while mean size at *Near* (92.8 mm ±1.85 SE) and *Far* (93.4 mm ±0.92 SE) sites did not differ (Tukey's $P > 0.05$). Mean sizes of lobsters *In* the Scorpion, Carrington, and Gull reserves were 102.2 (±0.67 SE), 100.7 (±0.47 SE), and 98.13 mm (± 0.36 SE), respectively. Outside reserves, the mean size of lobsters at *Near* and *Far* sites ranged from 89.7 (±0.60 SE; Gull *Near*) to 96.0 mm (±0.81 SE; 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 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 I pooled *Near* and *Far* data at all three reserves (KS, $P < 0.001$). Such results were not surprising because the port-sampling dataset consisted of an order of magnitude more lobsters than the trap sampling data.

Commercial effort distribution

I mapped the location of 617 total buoys at all *Near* and *Far* sites on four dates during the 2008-09 fishing season. Trap densities within these sites were not statistically different (one-way ANOVA, $F_{1,18} = 1.61$, $P = 0.22$; Table A6). Traps were generally distributed along-shore, although the total number and position changed with time, and I 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-MPA 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 I 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 towards larger size classes, and approximately four-eight times greater trap yield (lobster trap^{-1}) 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 eight-fold increase from 1979 to 2002 (reserve implemented in 1971). However, surveys conducted in 2002 reported by Parnell et al. did not reveal significantly higher densities of legal size *P. interruptus* inside versus outside the same reserve. This disparity in temporal versus 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. 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 spatio-temporal data.

The trap yield increases that I 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 ~5 times greater than those from NPS surveys, relative increases inside versus outside were nearly identical (Fig. 3). Our density estimates may have been higher than those of NPS because I 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 versus 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 spatio-temporal 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 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). To our knowledge, no study has combined before versus after data across replicate reserves, even though spatio-temporal 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 I 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.

I did not observe higher trap yield or effort at sites *Near* versus *Far* from reserve borders, and therefore conclude that spillover did not significantly influence trap yield or effort distribution outside reserves. A similar result indicating 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 (est. 1971) reserve in La Jolla, California, developed and intensified in the latter stages of the 2007-08 fishing season and was associated with complex habitat features near the reserve boundary (Parnell et al. 2010). I 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 above, 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 Bertalannfy growth parameters k and L_∞ (*see also* Sparre and Venema 1998). I applied the Beverton and Holt (1956) formula to our port sampling data (Fig. 5) and estimates of k (0.24) and L_∞ (103.3 mm) from a mark-recapture growth study (Kay, unpublished data), and I estimated a Z value of 0.49 for female lobsters at Santa Cruz Island (estimates for male lobsters not available). Although I were unable to directly estimate k and L_∞ for Santa Rosa Island sites, initial data from Santa Rosa indicate similar growth at both islands. Consequently, the larger mean size in commercial catches (Fig. 5) suggests that Z at Santa Rosa is lower than at Santa Cruz Island. This conclusion is supported by size structure data for Carrington *In* that were larger than at the Santa Cruz Island *In* sites (Fig. 5), thereby suggesting a lower historical fishing pressure that is further supported by the LEK of our fishery partners and attributed to extreme weather exposure (especially northwest winter swells and storms that enter the Santa Barbara Channel; Fig. 1). Our estimate of Z for *P. interruptus* within the Channel Island reserve network (0.49) 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 $Z = 0.93\text{-}1.24$ for *Panulirus polyphagus* in India; and Caputi et al. (2008) reported $Z = 1.42\text{-}2.12$ for *Panulirus cygnus* in three zones off Western Australia (I converted from their harvest rates of 70-85% and natural mortality = 0.22). The relatively moderate *Z* value that I 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 I 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, I explicitly tested the predictions of spillover as a process driven by non-seasonal 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 independent approaches represents an important frontier for CFR.

Our study is a valuable contribution to studies of reserve-fishing interactions because I demonstrate the potential for CFR to improve ecological assessments that inform policy. Fishery dependent methods and metrics enhanced this study by allowing me to perform a before versus 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, I 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 US 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 upwards (from ~$9 to $17US per pound from the 2006-07 to 2010-11 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 I 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 CA 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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LITERATURE CITED

Abesamis, R., G. Russ, and A. Alcala. 2006. Gradients of abundance of fish across no-take marine reserve boundaries: evidence from Philippine coral reefs. Aquatic Conservation: Marine and Freshwater Ecosystems 16:349-371.

Abesamis, R., and G. Russ. 2005. Density-dependent spillover from a marine reserve: long-term evidence. Ecological Applications 15:1798-1812.

Acosta, C. 2001. Assessment of the functional effects of a harvest refuge on spiny lobster and queen conch populations at Glover's Reef, Belize. Proceedings of the Gulf and Caribbean Research Institute 52:212-221.

Agardy, T., P. Bridgewater, M. Crosby, J. Day, P. Dayton, R. Kenchington, D. Laffoley, P. McConney, P. Murray, J. Parks, and L. Peau. 2003. Dangerous targets? Unresolved issues and ideological clashes around marine protected areas. Aquatic Conservation: Marine and Freshwater Ecosystems 13:353-367.

Babcock, R., N. Shears, A. Alcala, N. Barrett, G. Edgar, K. Lafferty, T. McClanahan, and G. Russ. 2010. Decadal trends in marine reserves reveal differential rates of change in direct and indirect effects. Proceedings of the National Academy of Sciences:107:18256-18261.

Barrett, N., C. Buxton, and C. Gardner. 2009. Rock lobster movement patterns and population structure within a Tasmanian marine protected area inform fishery and conservation management. Marine and Freshwater Research 60:417-425.

Beverton, R., and S. Holt. 1956. A review of methods for estimating mortality rates in exploited fish populations, with special reference to sources of bias in catch sampling. Rapports et Proces-Verbaux des Reunions (Consiel Permanent International pour l'Exploration de la Mer) 140:67-83.

Botsford, L., D. Brumbaugh, C. Grimes, J. Kellner, J. Largier, M. 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.

Branch, T., O. Jensen, D. Ricard, Y. Ye, and R. Hilborn. 2011. Contrasting global trends in marine fishery status obtained from catches and from stock assessments. Conservation Biology – early view online: http://onlinelibrary.wiley.com/doi/10.1111/j.1523-1739.2011.01687.x/abstract

Caddy, J., J. Csirke, S. Garcia, and R. Grainger. 1998. How pervasive is "fishing down marine food webs"? Science 282:1383a.

Caputi, N., R. Melville-Smith, S. de Lestang, J. How, A. Thomson, P. Stephenson, I. Wright, and K. Donohue. 2008. Draft Stock Assessment for the West Coast Rock Lobster Fishery.

CDFG (California Department of Fish and Game). 2008. Channel Islands Marine Protected Areas: First 5 Years of Monitoring: 2003-2008. (www.dfg.ca.gov/marine)

Conway, F., and C. Pomeroy. 2006. Evaluating the human - as well as the biological - objectives of cooperative fisheries research. Fisheries 31:447-454.

Côté, I., I. Mosqueira, and J. Reynolds. 2001. Effects of marine reserve characteristics on the protection of fish populations: a meta analysis. Journal of Fish Biology 59 Supplement A:178-189.

Davis, G., D. Kushner, J.M. Mondragon, J.E. Mondragon, D. Lerma, and D. Richards. 1997. Kelp Forest Monitoring Handbook Volume 1: Sampling Protocol. Channel Islands National Park – National Park Service. Ventura, California. (http://science.nature.nps.gov/im/units/chis/Reports_PDF/Marine/KFM-HandbookVol1.pdf)

Dayton, P., M. Tegner, P. Edwards, and K. Riser. 1998. Sliding baselines, ghosts, and reduced expectations in kelp forest communities. Ecological Applications 8:309-322.

DeMartini, E. 1993. Modeling the potential of fishery reserves for managing Pacific coral reef fishes. Fishery Bulletin 91:414-427.

Edgar, G., and N. Barrett. 1997. Short term monitoring of biotic change in Tasmanian marine reserves. Journal of Experimental Marine Biology and Ecology 213:261-279.

Edgar, G., and N. Barrett. 1999. Effects of the declaration of marine reserves on Tasmanian reef fishes, invertebrates and plants. Journal of Experimental Marine Biology and Ecology 242:107-144.

FAO. 2007. Report and Documentation of the Expert Workshop on Marine Protected Areas and Fisheries Management: Review of Issues and Considerations. FAO Fisheries Report No. 825. FAO, Rome.

Follesa, M., D. Cuccu, R. Cannas, S. Cabiddu, M. Murenu, A. Sabatini, and A. Cau. 2008. Effects of marine reserve protection on spiny lobster (*Palinurus elephas* Fabr., 1787) in a central western Mediterranean area. Hydrobiologia 606:63-68.

Forcada, A., C. Valle, P. Bonhomme, G. Criquet, G. Cadiou, P. Lenfant, and J. Sánchez-Lizaso. 2009. Effects of habitat on spillover from marine protected areas to artisinal fisheries. Marine Ecology Progress Series 379:197-211.

Freeman, D., A. MacDiarmid, and R. Taylor. 2009. Habitat patches that cross marine reserve boundaries: consequences for the lobster *Jasus edwarsii*. Marine Ecology Progress Series 388:159-167.

Goñi, R., S. Adlerstein, D. Alvarez-Berastegui, A. Forcada, O. Reñones, G. Criquet, S. Polti, G. Cadiou, C. Valle, P. Lenfant, P. Bonhomme, A. Pérez-Ruzafa, J. Sánchez-Lizaso, J. García-Charton, G. Bernard, V. Stelzenmüller, and S. Planes. 2008. Spillover from six western

Mediterranean marine protected areas: evidence from artisinal fisheries. Marine Ecology Progress Series 366:159-174.

Goñi, R., R. Hilborn, D. Díaz, S. Mallol, and S. Alderstein. 2010. Net contribution of spillover from a marine reserve to fishery catches. Marine Ecology Progress Series 400:233-243.

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 308:207-219.

Goñi, R., O. Reñones, and A. Quetglas. 2001. Dynamics of a protected western Mediterranean population of the European spiny lobster *Palinurus elephas* (Fabricius, 1787) assessed by trap surveys. Marine and Freshwater Research 52:1577-1587.

Guénette, S., T. Lauck, and C. Clark. 1998. Marine reserves: from Beverton Holt to the present. Reviews in Fish Biology and Fisheries 8:251-272.

Guenther, C. 2010. A Socio-ecological Analysis of Marine Protected Areas and Commercial Lobster Fishing in the Santa Barbara Channel, California. Ph.D. dissertation. University of California, Santa Barbara.

Gutiérrez, N., R. Hilborn, and O. Defeo. 2011. Leadership, social capital and incentives promote successful fisheries. Nature 470:386-389.

Halpern, B. 2003. The impact of marine reserves: do reserves work and does reserve size matter? Ecological Applications 13 Supplement:S117-S137.

Halpern, B., and R. Warner. 2002. Marine reserves have rapid and lasting effects. Ecology Letters 5:361-366.

Hamilton, L., and O. Otterstad. 1998. Demographic change and fisheries dependence in the Northern Atlantic. Human Ecology Review 5:16-22.

Hampton, J., J. Sibert, P. Kleiber, M. Maunder, and S. Harley. 2005. Decline of Pacific tuna populations exaggerated? Nature 434:E1.

Harmelin-Vivien, M., L. Le Diréach, J. Bayle-Sempere, E. Charbonnel, J. García-Charton, D. Ody, A. Pérez-Ruzafa, O. Reñones, P. Sánchez-Jerez, and C. Valle. 2008. Gradients of abundance and biomass across reserve boundaries in six Mediterranean marine protected areas: Evidence of fish spillover? Biological Conservation 141:1829-1839.

Hartley, T., and R. Robertson. 2009. Stakeholder collaboration in fisheries research: integrating knowledge among fishing leaders and science partners in northern New England. Society & Natural Resources 22:42-55.

Hilborn, R., T. Branch, B. Ernst, A. Magnusson, C. Minte-Vera, M. Scheuerell, and J. Valero. 2003. State of the world's fisheries. Annual Review of Environment and Resources 28:359-399.

Hilborn, R., F. Micheli, and G. De Leo. 2006. Integrating marine protected areas with catch regulation. Canadian Journal of Fisheries and Aquatic Sciences 63:642-649.

Hilborn, R., K. Stokes, J. Maguire, T. Smith, L. Botsford, M. Mangel, J. Orensanz, A. Parma, J. Rice, J. Bell, K. Cochrane, S. Garcia, S. Hall, G. Kirkwood,

K. Sainsbury, G. Stefansson, and C. Walters. 2004. When can marine reserves improve fisheries mangement? Ocean & Coastal Management 47:197-205.

Iacchei, M., P. Robinson, and K. Miller. 2005. Direct impacts of commercial and recreational fishing on spiny lobster, *Panulirus interruptus*, populations at Santa Catalina Island, California, United States. New Zealand Journal of Marine and Freshwater Research 39:1201-1214.

Jackson, J., M. Kirby, W. Berger, K. Bjorndal, L. Botsford, B. Bourque, R. Bradbury, R. Cooke, J. Erlandson, J. Estes, T. Hughes, S. Kidwell, C. Lange, H. Lenihan, J. Pandolfi, C. Peterson, R. Steneck, M. Tegner, and R. Warner. 2001. Historical overfishing and the recent collapse of coastal ecosystems. Science 293:629-637.

Kagwade, P. 1993. Stock assessment of the spiny lobster *Panulirus polyphagus* (Herbst) off north-west coast of India. Indian Journal of Fisheries 40:63-73.

Kaunda-Arara, B., and G. Rose. 2004. Effects of marine reef National Parks on fishery CPUE in Coastal Kenya. Biological Conservation 118:1-13.

Kellner, J., I. Tetreault, S. Gaines, and R. Nisbet. 2007. Fishing the line near marine reserves in single and multispecies fisheries. Ecological Applications 17:1039-1054.

Kelly, S., and A. MacDiarmid. 2003. Movement patterns of mature spiny lobsters, *Jasus edwarsii*, from a marine reserve. New Zealand Journal of Marine and Freshwater Research 37:149-158.

Kelly, S., D. Scott, and A. MacDiarmid. 2002. The value of a spillover fishery for spiny lobsters around a marine reserve in northern New Zealand. Coastal Management 30:153-166.

Kelly, S., D. Scott, A. MacDiarmid, and R. Babcock. 2000. Spiny lobster, *Jasus edwarsii*, recovery in New Zealand marine reserves. Biological Conservation 92:359-369.

Lester, S., B. Halpern, K. Grorud-Colvert, J. Lubchenco, B. Ruttenberg, S. Gaines, S. Airame, and R. Warner. 2009. Biological effects within no-take marine reserves: a global synthesis. Marine Ecology Progress Series 384:33-46.

Linnane, A., R. McGarvey, and J. Feenstra. 2009a. Northern Zone Rock Lobster (*Jasus edwarsii*) Fishery. Fisheries assessment report to PIRSA. South Australian Research and Development Institute, Adelaide, South Australia.

Linnane, A., R. McGarvey, and J. Feenstra. 2009b. Southern Zone Rock Lobster (*Jasus edwarsii*) Fishery. A report to PIRSA. South Australian Research and Development Institute, Adelaide, South Australia.

Lipcius, R., W. Stockhausen, and D. Eggleston. 2001. Marine reserves for Caribbean spiny lobster: empirical evaluation and theoretical metapopulation recuitment dynamics. Marine and Freshwater Research 52:1589-1598.

Lotze, H., H. Lenihan, B. Bourque, R. Bradbury, R. Cooke, M. Kay, S. Kidwell, M. Kirby, C. Peterson, and J. Jackson. 2006. Depletion, degradation, and recovery potential of estuaries and coastal seas. Science 312:1806-1809.

Lubchenco, J., S. Palumbi, S. Gaines, and S. Andelman. 2003. Plugging a hole in the ocean: the emerging science of marine reserves. Ecological Applications 13 Supplement:S3-S7.

MacDiarmid, A. 1991. Seasonal changes in depth distribution, sex ratio and size frequency of spiny lobster *Jasus edwarsii* on a coastal reef in northern New Zealand. Marine Ecology Progress Series 70:129-141.

MacDiarmid, A., and P. Breen. 1993. Spiny lobster population change in a marine reserve. Pages 47-56 *in* C. Battershill, editor. Proceedings of the Second International Temperate Reef Symposium, 7-10 January 1992, Auckland, New Zealand. NIWA Marine, Wellington.

Marí, M., D. Díaz, P. Abelló, and M. Zabala. 2002. Avaluació temporal de les poblacions de llagosta (*P. elephas*) en les Illes Medes. Pages 62-69 *in* M. Zabala, editor. Evolució del patrimoni natural de les Illes Medes. Technical Report: Direcció General de Pesca Marítima, Generalitat de Catalunya.

Mayfield, S., G. Branch, and A. Cockroft. 2005. Role and efficacy of marine protected areas for the South African rock lobster, *Jasus lalandii*. Marine and Freshwater Research 56:913-924.

McCay, J., and S. Jentoft. 1996. From the bottom up: participatory issues in fisheries management. Society & Natural Resources 9:237-250.

McClanahan, T., and S. Mangi. 2000. Spillover of exploitable fishes from a marine park and its effects on the adjacent fishery. Ecological Applications 10:1792-1805.

Milich, L. 1999. Resource mismanagement versus sustainable livelihoods: the collapse of the Newfoundland cod fishery. Society & Natural Resources 12:625-642.

Moffitt, E., L. Botsford, D. Kaplan, and M. O'Farrell. 2009. Marine reserve networks for species that move within a home range. Ecological Applications19:1835-1847.

Morgan, L., L. Botsford, S. Wing, and B. Smith. 2000. Spatial variability in growth and mortality of the red sea urchin, *Strongylocentrotus franciscanus*, in northern California. Canadian Journal of Fisheries and Aquatic Sciences 57:980-992.

Mullon, C., P. Freon, and P. Curry. 2005. The dynamics of collapse in world fisheries. Fish and Fisheries 6:111-120.

Murawski, S., R. Methot, and G. Tromble. 2007. Biodiversity loss in the ocean: how bad is it? Science 316:1281.

Murawski, S., S. Wigley, M. Fogarty, P. Rago, and D. Mountain. 2005. Effort distribution and catch patterns adjacent to temperate MPAs. ICES Journal of Marine Science 62:1150-1167.

Myers, R., J. Hutchings, and N. Barrowman. 1997. Why do fish stocks collapse? The example of cod in Atlantic Canada. Ecological Applications 7:91-106.

Myers, R., and B. Worm. 2003. Rapid worldwide depletion of predatory fish communities. Nature 423:280-283.

NRC (National Research Council). 2004. Cooperative Research in the National Marine Fisheries Service. National Academies Press, Washington DC.

Osenberg, C., B. Bolker, J.White, C. St. Mary, and J. Shima. 2006. Statistical issues and study design in ecological restorations: lessons learned from marine reserves. Pages 280-302 in: Foundations of Restoration Ecology, DA Falk, MA Palmer, and JB Zedler, eds. Island Press, Washington.

Pande, A., A. MacDiarmid, P. Smith, R. Davidson, R. Cole, D. Freeman, S. Kelly, and J. Gardner. 2008. Marine reserves increase the abundance and size of blue cod and rock lobster. Marine Ecology Progress Series 366:147-158.

Parnell, E., C. Lennert-Cody, L. Green, L. Stanley, and P. Dayton. 2005. Effectiveness of a small marine reserve in southern California. Marine Ecology Progress Series 296:39-52.

Parnell, E., Dayton, P., and F. Margiotta. 2006. Spatial and temporal patterns of lobster trap fishing: a survey of fishing effort and habitat structure. Bulletin of the Southern California Academy of Sciences 106:27-37.

Parnell, E., Dayton, P., Fisher, R., Loarrie, C., and R. Darrow. 2010. Spatial patterns of fishing effort off San Diego: implications for zonal management and ecosystem function. Ecological Applications 20:2203-2222.

Parrish, R. 1999. Marine reserves for fisheries management: why not? California Cooperative Oceanic Fisheries Reports 40:77-86.

Pauly, D., V. Christensen, J. Dalsgaard, R. Froese, and F. Torres. 1998. Fishing down marine food webs. Science 279:860-863.

Pauly, D., V. Christensen, S. Guénette, T. Pitcher, U. Rashid Sumaila, C. Walters, R. Watson, and D. Zeller. 2002. Towards sustainability in world fisheries. Nature 418:689-695.

Pew. 2003. Our Living Oceans: Charting a Course for Sea Change. Pew Oceans Commission, Washington, D.C.

Polacheck, T. 1990. Year around closed areas as a mangement tool. Natural Resource Modeling 4:327-354.

Roberts, C., J. Bohnsack, F. Gell, J. Hawkins, and R. Goodridge. 2001. Effects of marine reserves on adjacent fisheries. Science 294:1920-1923.

Russ, G., A. Alcala, A. Maypa, H. Calumpong, and A. White. 2004. Marine reserve benefits local fisheries. Ecological Applications 14:597-606.

Sale, P., R. Cowen, B. Danilowicz, G. Jones, J. Kritzer, K. Lindeman, S. Planes, N. Polunin, G. Russ, Y. Sadovy, and R. Steneck. 2005. Critical science gaps impede use of no-take fishery reserves. Trends in Ecology and Evolution 20:74-80.

Sánchez-Lizaso, J., R. Goñi, O. Reñones, J. García-Charton, R. Galzin, J. Bayle, P. Sánchez-Jerez, A. Pérez-Ruzafa, and A. Ramos. 2000. Density dependence in marine protected populations: a review. Environmental Conservation 27:144-158.

Sethi, S., T. Branch, and R. Watson. 2010. Global fishery development patterns are driven by profit but not trophic level. Proceedings of the National Academy of Sciences 107:12163-12167.

Shears, N., R. Grace, N. Usmar, V. Kerr, and R. Babcock. 2006. Long-term trends in lobster populations in a partially protected vs. no-take marine park. Biological Conservation 132:222-231.

Sparre, P., and S. Venema. 1998. Introduction to Tropical Fish Stock Assessment. FAO Fisheries Technical Paper 306/1 Rev. 2. FAO, Rome.

Stobart, B., R. Warwick, C. González, S. Mallol, D. Díaz, O. Reñones, and R. Goñi. 2009. Long term and spillover effects of a marine protected area on an exploited fish community. Marine Ecology Progress Series 384:47-60.

Swain, D., and E. Wade. 2003. Spatial distribution of catch and effort in a fishery for snow crab (*Chionoecetes opilio*): tests of predictions of the ideal free distribution. Canadian Journal of Fisheries and Aquatic Sciences 60:897-909.

Taylor, B., and J. McIlwain. 2010. Beyond abundance and biomass, effects of marine protected areas on the demography of a highly exploited reef fish. Marine Ecology Progress Series 411:243-258.

Tetreault, I., and R. Ambrose. 2007. Temperate marine reserves enhance targeted but not untargeted fishes in multiple no-take MPAs. Ecological Applications 17:2251-2267.

Tupper, M. 2007. Spillover of commercially valuable reef fishes from marine protected areas in Guam, Micronesia. Fishery Bulletin 106:527-537.

UN. 2002. Report of the World Summit on Sustainable Development. United Nations, New York.

UNEP-WCMC. 2008. National and Regional Networks of Marine Protected Areas: A Review of Progress. United Nations Environment Programme World Conservation Monitoring Centre, Cambridge.

US Commission on Ocean Policy. 2004. An Ocean Blueprint for the 21st Century. Final Report. US Commission on Ocean Policy. Washington DC.

Walters, C. 2003. Folly and fantasy in the analysis of spatial catch rate data. Journal of Canadian Fisheries and Aquatic Sciences 60:1433-1436.

Walters, C., 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 64:1009-1018.

Willis, T., and R. Millar. 2005. Using marine reserves to estimate fishing mortality. Ecology Letters 8:47-52.

Willis, T., R. Millar, R. Babcock, and N. Tolimieri. 2003. Burdens of evidence and the benefits of marine reserves: putting Descartes before des horse? Environmental Conservation 30:97-103.

Wilson, J., J. Prince, and H. Lenihan. 2010. A management strategy for sedentary nearshore species that uses marine protected areas as a reference. Marine and Coastal Fisheries: Dynamics, Management and Ecosystem Science 2:14-27.

Zar, J. 1999. Biostatistical Analysis. Prentice Hall. Upper Saddle Hall, New Jersey.

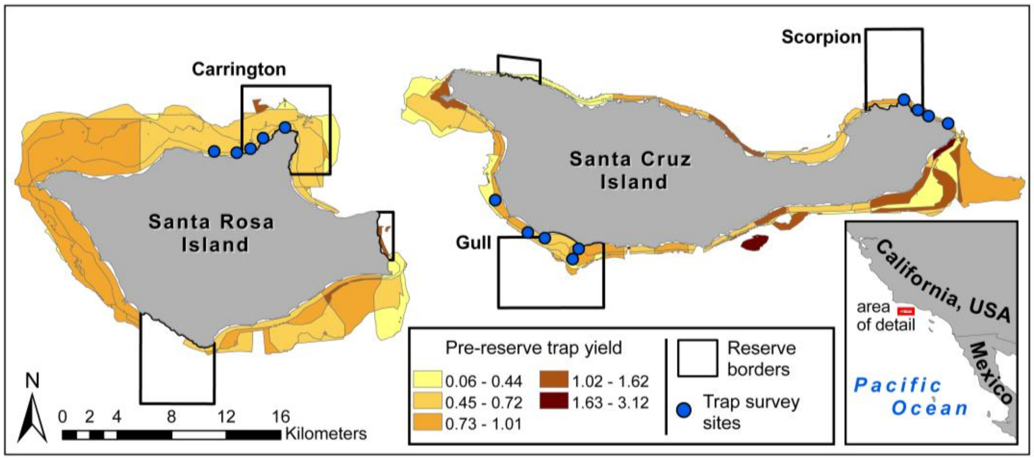

Figure 1.1. Map of sites where collaborative lobster trapping surveys took place (blue dots) at Santa Cruz and Santa Rosa Islands in the Southern California Bight (inset). Also shown are marine reserves (black rectangles) and polygons representing area-specific pre-reserve lobster trap yields (mean number of legal sized lobsters trap^{-1}) during the period from 1998-2002, as calculated from analysis of commercial lobster logbooks.

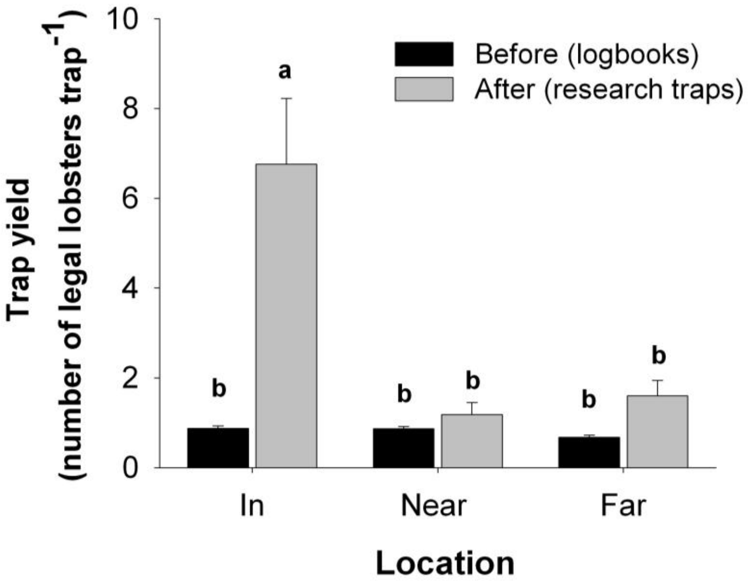

Figure 1.2. Mean number (± SE) of legal sized (≥82.5 mm) lobsters caught in replicate traps at sites within (*In*), immediately adjacent (*Near*), and 2-6 km distant (*Far*) three replicate Channel Island marine reserves. Data describing conditions before and after reserve implementation are from analysis of commercial logbooks and collaborative trapping surveys, respectively. Letters represent results of Tukey's post-hoc test (a > b at $P < 0.05$).

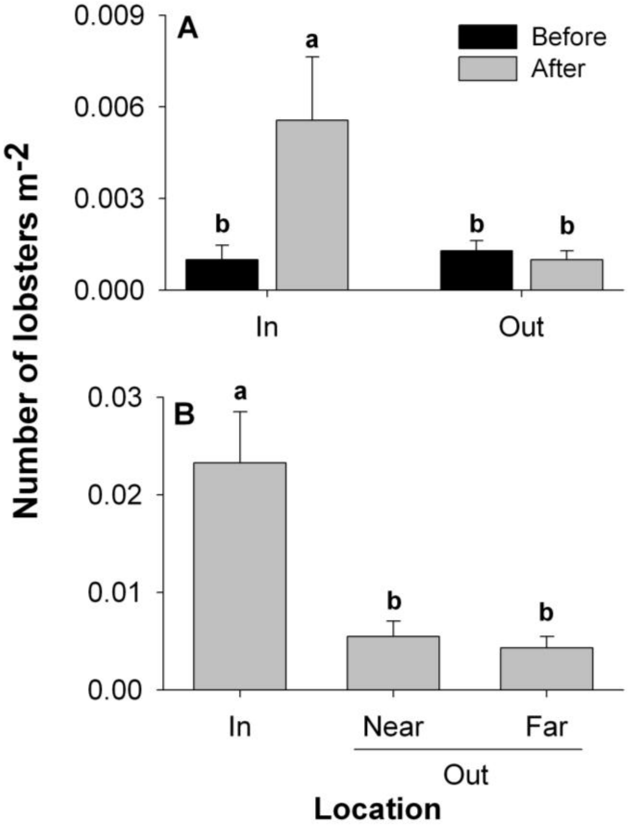

Figure 1.3. The mean number of lobsters m^{-2} (± SE) observed on visual SCUBA surveys conducted by (A) the National Park Service (NPS) kelp forest monitoring program and (B) M. Kay. NPS data include all sizes of lobsters observed, while data from our research team includes only legal sized lobsters. Letters represent results of Tukey's post-hoc test (a > b at $P < 0.05$).

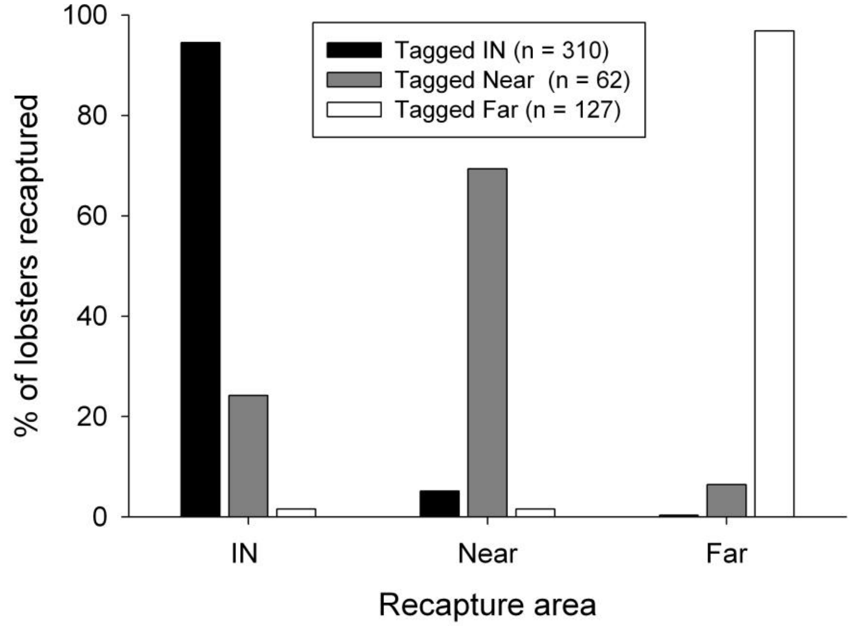

Figure 1.4. The percentage of lobsters that were tagged, and subsequently recaptured, in each of the three survey locations (*In*, *Near*, *Far*). Data for each survey location are pooled from all three reserves. Legend indicates original tagging locations and the number of lobsters recaptured from each tagging location (not the total number tagged in each location). Data are from lobsters tagged and recaptured during research trapping surveys prior to the 2007-08 and 2008-09 fishing seasons.

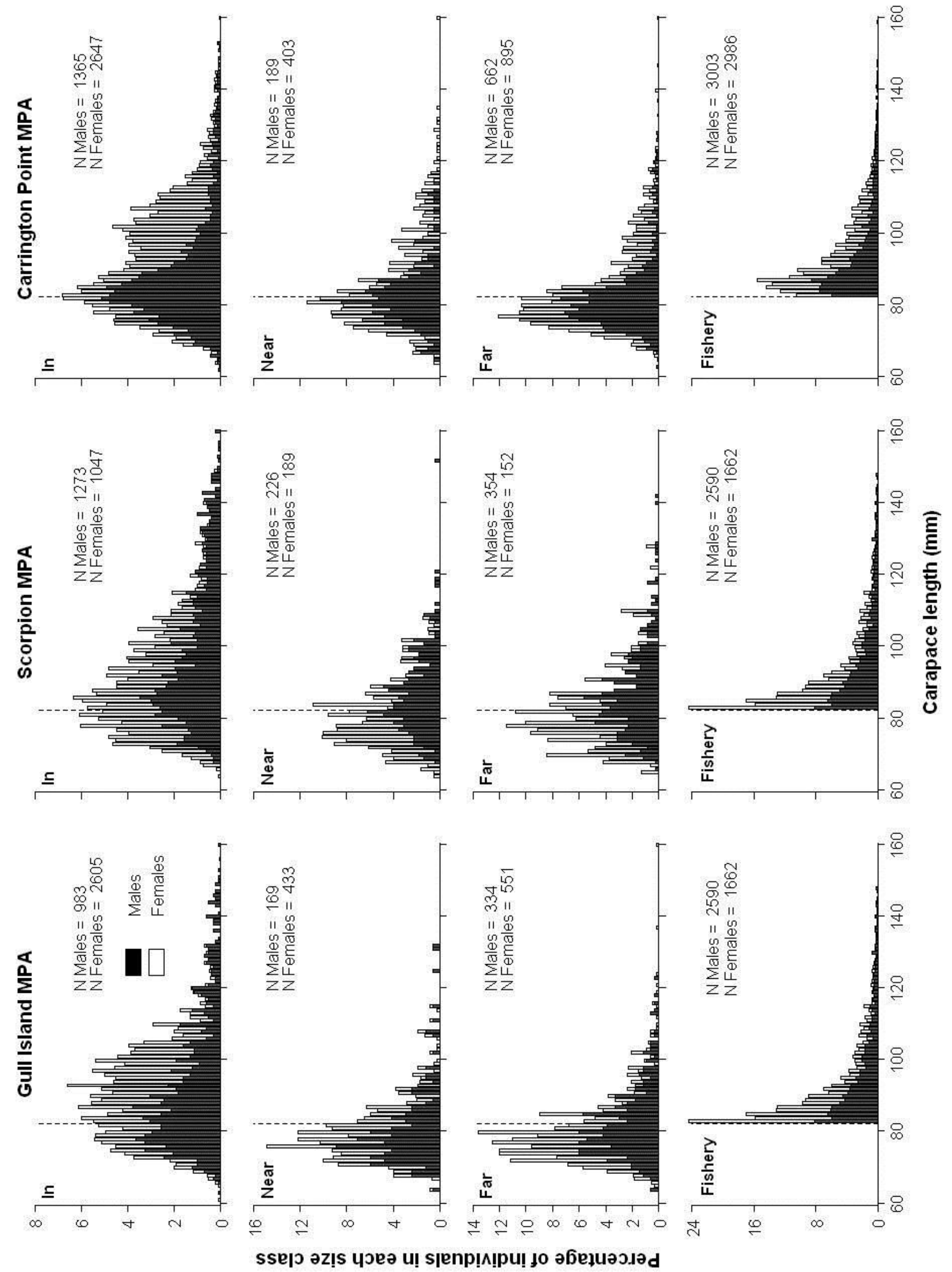

Figure 1.5. Length frequency histograms for lobsters caught during collaborative trapping surveys and concurrent port sampling of commercial catch from Santa Cruz and Santa Rosa Islands.

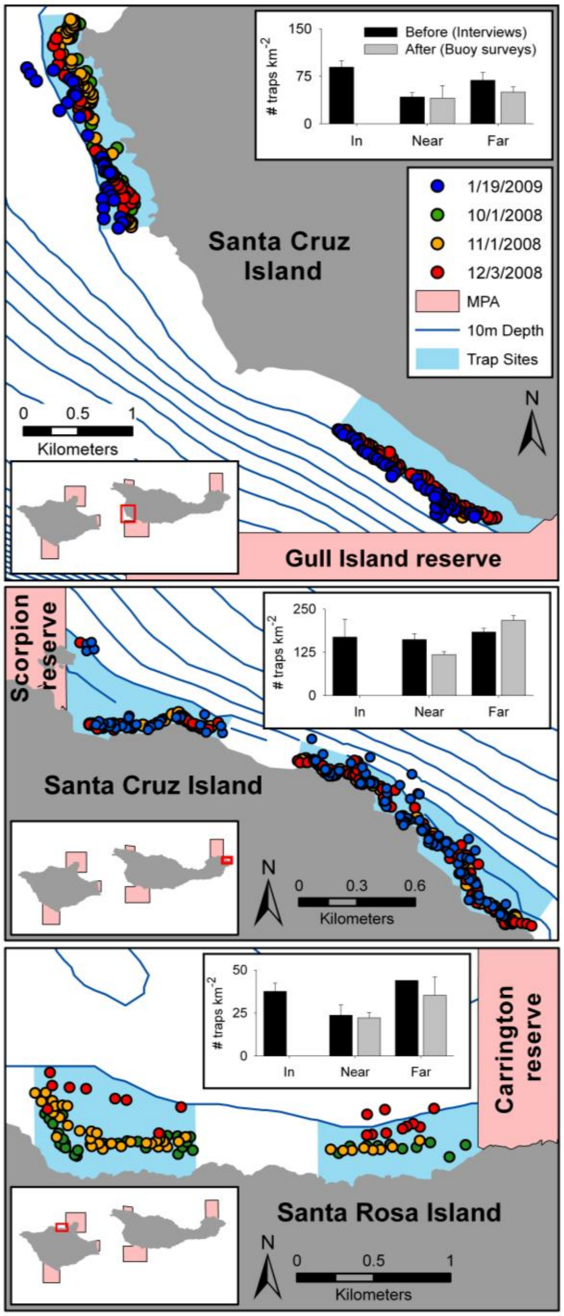

Figure 1.6. Commercial effort (buoy) distribution at each reserve site on four (Gull) or three (Scorpion, Carrington) dates during the 2008-09 fishing season. Blue polygons are areas where collaborative trapping took place. Commercial effort was not sampled between the *Near* and *Far* polygons (sites), but was qualitatively similar. Insets show effort patterns (mean ± SE) before and after reserve implementation, as measured from fisherman interviews and buoy surveys, respectively.

APPENDIX A

TABLE A1. Results of two-way ANOVA testing for the effects of location (*In*, *Near,* and *Far* from reserves) and time (*Before* vs. *After* reserves), and their interaction, on the trap yield of legal sized lobsters (see Fig. 2). df = degrees of freedom; ss = sum of squares; ms = mean square; *F* = *F*-ratio.

Source	df	ss	ms	*F*	*P*
Location (L)	2	1.47	0.76	18.62	0.0002
Time (T)	1	1.89	1.89	47.68	0.0001
L x T	2	1.26	0.63	15.99	0.0004
Residual	12	0.47	0.04		
Total	17	5.10			

TABLE A2 a and b. Results of ANOVAs testing for the effect of location and time (a), or location only (b), on the total number (a) or number of legal (b) lobsters observed on SCUBA transects (see Fig. 3A and B).

Source	df	ss	ms	*F*	*P*
a) National Park Service data					
Location (L)	1	$9.8e^{-5}$	0.001	10.86	0.001
Time (T)	1	$9.9e^{-5}$	0.001	10.96	0.001
L x T	1	$1.3e^{-4}$	0.001	14.13	<0.001
Residual	117	$1.0e^{-3}$	$9.1e^{-6}$		
Total	120	$1.2e^{-3}$			
b) Surveys at trapping sites					
Location	2	3.75	1.87	10.56	0.011
Residual	6	1.07	0.18		
Total	8	4.82			

TABLE A3. Results of Welch's ANOVAs testing for differences in trap yield for traps deployed by actively fishing commercial lobstermen vs. collaborating fishermen/researchers (Trpr.). Yield per trap for commercial fishermen was calculated from logbooks. This comparison was repeated (once each during the 2006-07 and 2007-08 seasons), and was conducted to ensure comparability of fishery logbook data and research trapping data (see *Materials and Methods*).

	2006-07					2007-08				
Source	df	ss	ms	*F*	*P*	df	ss	ms	*F*	*P*
Trpr.	1	0.001	0.001	0.007	0.93	1	0.14	0.14	1.75	0.19
Resid.	49	5.15	0.10			53	4.33	0.08		
Total	50	5.15				54	4.48			

TABLE A4. Results of ANOVA testing the assumption that commercial effort was not significantly different across locations (*In, Near, and Fa*r) before reserves.

Source	df	ss	ms	*F*	*P*
Location	2	0.24	0.122	1.43	0.26
Residual	25	2.14	0.086		
Total	27	2.39			

TABLE A5. Results of ANOVA testing for the effect of location (*In, Near, and Far*) on the mean size of all legal lobsters capture in traps.

Source	df	ss	ms	*F*	*P*
Location	2	0.011	0.006	8.94	0.016
Residual	6	0.004	0.001		
Total	8	0.015			

TABLE A6. Results of ANOVA testing for differences in commercial effort at locations *Near* vs. *Far* from reserve borders (see Fig. 6).

Source	df	ss	ms	*F*	*P*
Location	1	0.44	0.44	1.61	0.22
Residual	18	4.95	0.27		
Total	19	5.39			

CHAPTER 2

Controlling for Habitat Confirms Robust Reserve Effects and Gradients of Abundance Near Borders for California Spiny Lobster

INTRODUCTION

Concern for populations targeted by marine fisheries has increased in recent decades and has motivated the establishment of no-take marine reserves in coastal oceans worldwide (UNEP-WCMC 2008). Marine reserves work by eliminating (or reducing) fishing mortality inside their borders, and numerous empirical studies describe reserve effects such as increased size, abundance, and biomass of target organisms inside reserve borders (reviews by Côté et al. 2001, Halpern 2003, Lester et al. 2009). Reserve effects are often measured as average differences at sites categorically inside versus outside single reserves, but dynamics of marine populations and the effects of marine reserves are probably subject to high spatial variability (MacCall 1990, García-Charton and Pérez-Ruzafa 1999, Prince 2005, Stelzenmüller et al. 2007). Identifying and controlling for drivers of spatial variability provides critical information that improves predictions and assessments of reserve performance (Agardy et al. 2003, Sale et al. 2005). Two critical drivers are habitat characteristics and the distance of sampling sites from reserve borders (Stelzenmüller et al. 2007, Harmelin-Vivien et al. 2008).

Theory suggests that reserve effects can vary as a function of distance from reserve borders due to the emigration of organisms from reserves (spillover).

Spillover models predict gradients in relative abundance that peak near reserve centers, decline across borders into fished areas, and reach an asymptotic low value farther into fished areas (Kaunda-Arara and Rose 2004, Hilborn et al. 2006). Early empirical studies designed to test for gradients in abundance or catch rates (a proxy for abundance) across or near reserve borders offer some support for model predictions but in many cases gradients are absent (Chapman and Kramer 1999, Kaunda-Arara and Rose 2004, Abesamis et al. 2006, Goñi et al. 2006). The absence of gradients can be explained by factors other than the lack of spillover, and these include concentrated fishing effort near borders (*fishing the line*) and high organism mobility (Goñi et al. 2006, Abesamis et al. 2006, Kellner et al. 2007). Perhaps the most common explanation, which has been demonstrated in a very few but highly informative recent studies, is that spatial heterogeneity of habitat structure drives spatial patterns of abundance that alter or obscure spillover-driven gradients (Goñi et al. 2008, Harmelin-Vivien et al. 2008, Forcada et al. 2009).

Habitat structure is an essential consideration for assessments of area-based management strategies because it can profoundly influence local-scale demography (García-Charton and Pérez-Ruzafa 1999). Although relatively few marine reserve studies control for habitat structure heterogeneity, those that do so indicate that habitat can influence reserve effects. For example, the density and mean size of 7 and 13 fish species, respectively, were initially found to be greater inside a Barbados reserve than in nearby fished areas (Rakitin and Kramer 1996).

Subsequently, the same reserve was studied in a manner that controlled for the influence of habitat heterogeneity, and the same species sampled by Rakitin and Kramer (1996) were not statistically larger or more abundant inside the reserve (Chapman and Kramer 1999). Other studies indicate that fish assemblage characteristics (richness, diversity, abundance, or biomass) are higher inside reserves but vary significantly across habitat types (Grigg 1994, Friedlander et al. 2007, Harmelin-Vivien et al. 2008). Recent work in the Mediterranean Sea indicates that habitat heterogeneity near reserve borders modifies spillover effects on catch rates (Stelzenmüller et al. 2007, Forcada et al. 2009). Reserve studies that consider the role of habitat typically focus on categorical definitions (e.g., seagrass meadows, rocky reef, or sand) but small scale structural features within a given habitat type can also influence organism abundance and/or reserve effects (Harmelin-Vivien et al. 2008). Despite this evidence, few studies measure specific habitat structural features within habitat types at sampling sites, and consequently there is a need for empirical studies that describe and control for fine scale habitat features when exploring both the mean effects of reserves (i.e., differences at sites categorically inside vs. outside) and the spatial distribution of reserve effects.

Here I report the mean effects of reserves and the influence of distance from reserve borders on the number and size of California spiny lobster (*Panulirus interruptus*) trapped at sites across a reserve network at the Santa Barbara Channel Islands, California USA. Kay et al. (2008, *in press*) report increased trap yield, mean size, and larger population structure inside versus outside reserves at sites that were carefully selected in collaboration with commercial fishermen to have similar habitat and historical lobster catch. In this study, I explore how mean population effects on spiny lobsters change with distance from reserve borders, and I control for habitat variability across sites in two ways. First, I conducted visual habitat surveys at all sites to quantify fine scale habitat features that may influence lobster abundance. Second, I compared trap yields for legal sized lobsters with those for sublegal adults. Sublegal adult abundance is not directly reduced by fishing outside reserves, and sublegal abundance inside is not linked via reproduction to adult abundance on reefs sampled in this study because larvae of *P. interruptus* are distributed far from parental sites. Thus, our measurements of sublegal abundance provide a novel control for spatially variable factors (i.e., habitat) that could bias perceived reserve effects. The result is a robust case study of *P. interruptus* responses to reserve protection that informs theoretical predictions regarding how reserves influence populations at varying spatial scales.

MATERIALS AND METHODS

Site Description and Selection

Our study was conducted at sites associated with three marine reserves at the Santa Barbara Channel Islands (SBCI): Gull and Scorpion (Santa Cruz Island), and Carrington (Santa Rosa Island; Fig. 1). General characteristics of the SBCI marine reserve network (CDFG 2008), as well as the selection process for sites used in this study, are described elsewhere (Kay et al., *in press*). Briefly, however, scientists and commercial lobster fishermen worked collaboratively to identify reefs located inside and outside reserves and that had similar physical, ecological, oceanographic, and fishery catch characteristics. Ultimately, I selected four trapping sites associated with the Scorpion reserve, and I selected five at the larger Gull and Carrington reserves (14 total). Sites were spatially distributed near the center, immediately inside, adjacent outside, and far out (~2-6 km away) relative to a single border of each reserve (Fig. 1). I used GIS (ArcGIS 9.3.1, ESRI) to calculate the midpoint distance of each trapping site to the nearest reserve border.

Collaborative Trapping

We deployed 10-15 replicate lobster traps at each of the sites associated with the three individual reserves (duplicated sites in the center of Gull and Carrington reserves received the same approximate effort as a single site; total traps = 10-15 traps x 4 trapping sites = 40-60 traps per reserve). Traps were sampled every 1-4 days over a 1-3 month period at each site from August-December 2006, 2007 and 2008. Traps used in this study were identical to those used in the fishery for *P. interruptus* at SBCI. Traps were 91.5 x 122 x 45.7 cm tall; constructed of Riverdale® 2 x 4 inch (5.1 x 10.2 cm) mesh wire; attached at their base to a single 91.5 x 122 cm rectangular frame constructed from 1 inch (2.5 cm) diameter steel rod; and coated with a hydrocarbon asphalt sealant used by the fishery to prevent corrosion. The only difference between commercial traps and traps used in this study is that the latter did not have escape ports that allow the escape of sublegal lobsters. Traps were baited with ~500 gm of Pacific mackerel (*Scomber japonicus*) that was replaced in 1-L plastic bait capsules (1 per trap) after each sampling event.

In each trapping area, initial deployment of traps was conducted from a commercial lobster vessel or was guided by commercial lobstermen on the fishing grounds. Individual traps were placed haphazardly in stratified reef areas that were defined prior to fieldwork, and which were delineated by bathymetry, sand-rocky reef interfaces, and/or the extent of giant kelp *Macrocystis pyrifera*. As each trap was retrieved, I recorded the depth, time, date, and GPS coordinates, as well as the total number, sex, carapace length (nearest mm using vernier calipers) injuries (e.g., missing legs or antennae), and breeding condition of all lobsters in the trap. Additionally, lobsters were tagged with an individually numbered T-bar tag (TBA-2 standard, Hallprint Tags, Australia) 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 would persist through molting. I minimized stress to lobsters on deck by returning them to the ocean as quickly as possible, placing them in standing seawater, or shading traps with wet burlap sacks as lobsters were removed. After lobsters had been processed, they were returned to the exact location of capture and released by hand.

Habitat Surveys

We performed SCUBA surveys at each trapping site to identify and control for the potential influence of select habitat features on trap yield. During August-October 2008, I conducted 80 SCUBA transect surveys across 13 of the 14 trapping sites inside and outside of the reserves. At each site I conducted a minimum of 6 transect surveys, and transects were 45 m long x 10 m wide (450 m^2 x 6 transects per site = ≥ 2700 m^2 of reef surveyed at each site in Fig. 1). Divers recorded the total number of dens, caves, and the extent of linear crack that could be occupied by lobsters on each transect. These three features were selected based upon prior analyses that identify them as critical habitat features for determining lobster abundance on reefs at our Channel Islands trapping sites (Kay, *unpublished data*).

Dens were defined as any cave-like open space in solid rock or boulders that was enclosed on all sides except for one-three openings (openings no greater in diameter than the depth of the cave-like structure), and which one-three legal-sized lobsters (≥82.5 mm carapace length) could occupy and use as defensible space in the presence of predators. Caves were defined as openings whose inner diameter exceeded the diameter of the entrance and that could serve as refuge for four or more legal-sized lobsters. Linear crack was defined as any fissure that was deep enough to be occupied by a legal sized lobster but lacked the walls of a den or cave, such that a potential predator could approach a lobster from any direction in a 180° arc (in two-dimensional space) as opposed to the aperture of a den or cave entrance. A single diver (Kay) recorded these features on all transects to eliminate diver-based bias across sites.

Statistical approach

Our first objective was to compare trap performance (number of legal sized lobsters [≥82.5 mm carapace length], the number of sublegal lobsters, and the mean size of legal lobsters) inside versus outside the three reserves, and to simultaneously identify and control for the influence of the three fine-scale habitat features (dens, caves, and crack). To accomplish this, I specified the following multiple regression model:

$$Y = \alpha + \gamma Reserve + \beta X + \varphi Scorpion + \delta Carrington + \rho 2006 + \omega 2007 + \varepsilon \qquad (1)$$

where response variable Y represents either the number of legal sized (≥82.5 mm) lobsters per trap, the number of sublegal lobsters per trap, or the mean size of legal sized lobsters in traps (i.e., the model was run for each of the three response variables); α is the intercept (constant) in each model; *Reserve* is a dummy variable for traps inside any reserve, X is a column vector of the independent variables (trap depth, number of nights traps were deployed, number of dens, caves, and extent (meters) of linear crack on reefs at each site); *Scorpion* and *Carrington* are categorical variables for sites associated with the Scorpion and Carrington reserves, with Gull the omitted category; *2006* and *2007* are categorical variables for data collected during those years, with 2008 the omitted category; and ε is the error term (variance not explained by the model).

Coefficient γ describes the influence of location relative to reserve (inside vs. outside any of the three reserves) on the response variables, the coefficients in row vector β describe the influence of each independent variable (column vector X) on the number of legals, number of sublegals, and mean size of legal lobsters caught. The coefficients φ and δ account for the average differences in response variables by reserve using Gull as the basis for comparison; and ρ and ω account for the average differences in response variables by year using 2008 as the basis for comparison.

Our second objective was to test the relationship between trap performance and distances of trapping sites from reserve borders, and to simultaneously identify and control for the influence of the three fine-scale habitat features (dens, caves, and crack). The distance of each trapping area from the nearest reserve border was measured from the midpoint among traps at each area. These measurements replaced the *Reserve* dummy variable in Model (1), such that a new model was specified:

$$\begin{aligned} Y = \alpha + \theta\mathit{indist} + \gamma\mathit{outdist} + \beta X + \varphi\mathit{Scorpion} \\ + \delta\mathit{Carrington} + \rho\mathit{2006} + \omega\mathit{2007} + \varepsilon \qquad (2) \end{aligned}$$

where *indist* and *outdist* are distances of trapping areas inside and outside any reserve, respectively, and θ and γ describe the influence of distance from reserve borders on trap performance in those areas. All other terms in Model (2) are as described above for Model (1), such that the influence of distance from reserve borders was measured while controlling for the influence of site-specific habitat features.

Finally, I repeated our second objective (to test the relationship between trap performance and distances of trapping sites from reserve borders) through specification of the following model that allowed non-linear relationship between response and predictor variables:

$$\begin{aligned} Y = \alpha + \theta \mathit{indist} + \psi(\mathit{indist})^2 + \gamma \mathit{outdist} + \xi(\mathit{outdist})^2 + \beta X \\ + \varphi \mathit{Scorpion} + \delta \mathit{Carrington} + \rho \mathit{2006} + \omega \mathit{2007} + \varepsilon \end{aligned} \qquad (3)$$

where $(\mathit{indist})^2$ and $(\mathit{outdist})^2$ are the only new terms introduced, and the coefficients ψ and ξ estimate the extent of any non-linearity. All other terms are as described for Model (2).

After Models (1-3) were run as described above, they were repeated with one important alteration: the number of sublegal lobsters trap^{-1} was removed as a response variable and included in each model as a predictor variable. The models were the same in all other aspects. The two response variables for each model were (1) the number of legal lobsters trap^{-1} and (2) the mean size of legal lobsters trap^{-1}. Running the three models sequentially (i.e., excluding then including the number of sublegals trap^{-1} as a predictor variable) was fundamental to using sublegals trap^{-1} to control for habitat heterogeneity. Specifically, using the number of sublegals trap^{-1} as a response variable in Models (1-3) allowed me to determine if trap yield for sublegals changed with regard to trap location inside, outside, or with increasing distance form reserve borders (i.e., was influenced by the *Reserve*, *indist*, and *outdist* predictor variables). I predicted that sublegals should not be influenced by reserve protection, since they are not removed by fishing, such that any influence of the *Reserve*, *indist*, and *outdist* predictor variables is likely an artifact of habitat heterogeneity but not reserve effects *per se*. For models in which the number of sublegals trap^{-1} was a response variable, I determined *a priori* that significant coefficient values for the *Reserve*, *indist*, and *outdist* predictors would be interpreted to indicate that habitat was variable among sites and responsible for any statistically significant trends in sublegal abundance. This is important because habitat heterogeneity that influences sublegal abundance is likely to also influence abundance and mean size of legal lobsters. Therefore, using the number of sublegals trap^{-1} as a predictor variable in the second set of models provides a control for habitat features that may drive perceived reserve effects reported for legal lobsters.

For all models, numerical values for habitat features (caves, dens, crack) that were measured during SCUBA surveys are the averages from six transects at each trapping area, such that all traps at within an area were associated with a common score for each habitat variable. Similarly, the distance of each area from the nearest reserve border was measured as the average distance of all traps at an individual trapping area. Due to this averaging of trap distance and habitat scores, standard errors during the analyses were clustered for the 14 areas. This accounts for the fact that some covariates vary only at the level of the trapping area. Models were specified to be robust to heterogeneity of variance and non-normal distribution, and were estimated using STATA 9 (StataCorp, 2005). Statistical significance was determined at the 0.05 level.

RESULTS

Model (1) – Responses at sites categorically inside versus outside reserves

After controlling for all variables in our model, traps that were deployed inside reserves captured an average of 5.49 more legal lobsters trap^{-1} than those placed outside reserves, but only 0.92 more sublegal lobsters trap^{-1}, and for both response variables the differences were highly statistically significant (Table 1). These statistical results are also apparent in the raw data without controlling for any covariates (Figs. 2A, B). The number of legal lobsters caught was statistically influenced by the mean density of both dens and caves at each trapping site (predictor variables *Dens* and *Caves*), such that each additional den or cave per 450 m^2 had the marginal effect of increasing trap yield by 0.22 and 0.77 legal lobsters trap^{-1}, respectively (Table 1). In contrast, the number of meters of linear crack per 450 m^2 did not influence trap yield.

Model (1) indicates that reserves increased the carapace length of legal lobsters inside versus outside reserves by an average 6.77 mm, and the difference was highly significant (Table 1) and clearly represented in the raw data (Fig. 2C). The number of dens and extent of linear crack per 450 m^2 significantly influenced the mean size of legal lobsters trapped, such that each additional den and meter of crack resulted in a 0.21 and 0.07 mm increase in mean size, respectively. Mean size of legal lobsters trapped at Carrington was significant and 2.33 mm larger than at Gull (the omitted category).

Specification of Model (1) to include the number of sublegals $trap^{-1}$ as a predictor variable (Table 2) improved the explanatory power of the model (adjusted R^2 increased from 0.36 to 0.51), and still indicates that reserves significantly influence the number and mean size of legal lobsters $trap^{-1}$ despite the factors that caused sublegal trap yield to be higher inside than outside reserves. The coefficient describing the effect of the *Reserve* predictor on the *# legals* response variable was slightly lower than in the original model (4.81 vs. 5.49), and the difference (0.68) is similar to the coefficient value for the number of sublegals as a predictor (0.74), and indicates the extent to which *Reserve* in the original model was attributable to factors unrelated to reserve protection. The *Dens*, *Caves*, and *Crack* predictors remained significant as in the original specification (but with slightly different coefficient values), and *# sublegals* was a highly significant predictor for both response variables.

To summarize, Model (1) controls for the statistically significant influences of fine scale habitat features (e.g., *Dens*), reserve site location (*Gull*, *Scorpion*, or *Gull*), and season (years *2006-2008*), and indicates that all three response variables (*# legals*, *# sublegals*, and *mean size*) were significantly influenced by location inside versus outside reserves. Including the number of sublegals as a predictor variable in Model (1), which accounts for other unobserved habitat quality, improved the explanatory power of the model and increased the adjusted R^2 for the # *legals* response variable from 0.36 to 0.51, but had a much smaller impact on the explanatory power for mean size (adjusted R^2 increased from 0.20 to 0.22).

Model (2) – Influence of distance from borders (linear model)

Among trapping sites inside of marine reserves, the distance of individual sites from the nearest reserve border (predictor variable *indist)* strongly influenced the number of legal lobsters $trap^{-1}$ (Table 1), and the same trend is clearly present in the raw data (Fig. 3A). The statistically significant coefficient for *indist* ($\theta = 2.99$) indicates that 2.99 more legal lobsters $trap^{-1}$ were captured for every kilometer moved further inside reserves. Similarly, there was a significant relationship ($\theta = 0.78$) between distance inside borders and the number of sublegals $trap^{-1}$, but this statistical relationship is difficult to perceive in the raw data (Fig. 3B). For both legal and sublegal sized lobsters, there was no statistically significant relationship between trap yield and distance outside of reserve borders, but the number of nights that traps were deployed significantly influenced yield of both size categories (Table 1).

The relationship between mean size of legal sized lobsters in traps and the distance of trapping sites outside of reserve borders (*outdist*) was statistically significant, although this trend is not apparent in the raw data (Fig. 3C). The negative coefficient value for *outdist* ($\gamma = -1.53$) indicates that for each kilometer moved farther outside reserves the mean size of legal lobsters declined by 1.53 mm (Table 1). In contrast, there was no statistically significant relationship between legal lobster mean size and distance inside reserves. As with the # *legals* and *mean size* response variables in Model (1), the number and mean size of legal lobsters in Model (2) were significantly influenced by the number of dens observed on SCUBA transects. Specifically, for each additional den per $450m^2$ transect the number and mean size of legal lobsters in traps increased by 0.07 lobsters $trap^{-1}$ and 0.28 mm, respectively. Interestingly, each additional cave observed on transects resulted in a decreased mean size of 2.16 mm for legal lobsters in traps.

Specification of Model (2) to include # *sublegals* as a predictor variable (Table 2) confirms the highly statistically significant relationship between distance inside reserves and the number of legal sized lobsters $trap^{-1}$, and improved the explanatory power of the model (adjusted R^2 increased from 0.39 to 0.53) . The relationship between distance outside reserves and the mean size of lobsters in traps also remained significant, but the explanatory power of the model increased only slightly (adjusted R^2 increased from 0.17 to 0.19). Both response variables in the model were significantly influenced by the number of dens observed on SCUBA transects, such that for each additional den per $450m^2$ transect the number and mean size of legal lobsters in traps increased by 0.10 lobsters $trap^{-1}$ and 0.26 mm, respectively.

Model (3) – Influence of distance from borders (nonlinear model)

In the nonlinear model, neither the number of legal sized lobsters nor the number of sublegal lobsters captured trap^{-1} was significantly influenced by distance from borders inside or outside of reserves (Table 1). Similarly, the mean size of legal lobsters was not influenced by distance from reserve borders at sites inside reserves. Outside reserves, however, there was a significant relationship between distance from reserve borders and mean size of legals (Table 1), and coefficients for predictors *outdist* and (*outdist*)^2 were statistically significant. This result is consistent with distance-size relationship outside reserves reported for Model (2). Additionally, there was a statistically significant relationship between mean size and the number of dens per 450 m^2 transect, such that the addition of each den per 450m^2 resulted in an increased mean size of 0.29 mm. As in Models (1) and (2), there was a negative relationship between cave abundance and mean size. Specification of Model (3) to include # *sublegals* as a predictor variable (Table 2) increased the predictive power of the model but interpretation of how reserves influence response variables in the original model is largely unchanged.

DISCUSSION

Our effort to minimize and statistically control for habitat heterogeneity across sites strengthens our conclusion that trap performance in this study was indeed influenced by the non-habitat predictor variables in our models, most notably the average effect of trap location inside versus outside reserves (Fig. 2; Model [1]), and distance from reserve borders (Fig. 3; Models [2] and [3]). Accounting for such factors represents a major challenge to marine ecologists (García-Charton and Pérez-Ruzafa 1999, Sale et al. 2005) and affects stakeholder confidence in reserve science (Agardy et al. 2003). An important step in minimizing habitat bias was the inclusion of commercial fishermen whose local ecological knowledge (LEK; Hartley and Robertson 2009) was essential for identifying reefs with similar physical characteristics and historical fishing production (Kay et al. *in press*). Evidence that I were successful in selecting such reefs is suggested by catch patterns among sublegal lobsters, for which variation among sites was relatively low (Fig 3B).

Although differences in sublegal catch across sites was lower than for legal lobsters, sublegal trap yield nevertheless varied significantly for coefficients that describe the average effects of reserves (Table 1, Model [1], *Reserve* predictor) and the distance from reserve borders (Table 1, Model [2], *indist* predictor). These results are most likely driven by site specific habitat differences because sublegal lobsters are not taken in the commercial fishery. Thus, inclusion of *# sublegals* as a predictor variable (Table 2) provided a valuable additional control for habitat heterogeneity across sites. This is supported by the increased predictive power (i.e., higher adjusted R^2) of models that include the *# sublegals* predictor. Comparison of models with and without the *# sublegals* predictor (i.e., Table 1 vs. Table 2) suggests that perceived reserve effects for models without this predictor were partially driven by factors unrelated to reserve protection. For example, in the specification of Model (1) in which *# sublegals* was used as a predictor, the influence of the reserves on the # *legals* response variable was lower than in the original model (4.81 vs. 5.49). The difference (0.68) is similar to the coefficient value for the # *sublegals* predictor (0.74), and indicates that 0.68-0.74 of the 5.49 more lobsters trap^{-1} indicated by the *Reserve* coefficient in the original model (Table 1) was due to factors unrelated to reserve protection. Similarly, the *indist* coefficient was higher ($\theta = 2.99$) in the original Model (2) than in the specification with sublegals as a predictor ($\theta = 2.43$), and in the latter model the # *sublegals* predictor was highly significant. These facts indicate that the perceived effect of distance from reserve borders reported in Table 1 was partially driven by factors that also influence the trap yield of sublegal lobsters (i.e., factors unrelated to reserve protection).

Our conclusion that variable sublegal trap yield is in fact caused by site-specific habitat differences, which in turn account for the observed influence of *Reserve* and *indist* predictors on sublegal catch, is vulnerable to two alternative explanations. The first is that fishing does indeed cause mortality among sublegals due to interactions with fishing gear, predators, or handling stress (e.g., Gooding 1985, DiNardo et al. 2002). This seems unlikely because traps used in the commercial fishery are equipped (by law) with escape ports for sublegal lobsters, but escape ports were absent on the traps I used in our sampling. Consequently, traps used in this study captured lobster size classes that are not (or minimally) captured by standard commercial traps (Kay, *unpublished data*). The second alternative is that increased biomass of adults inside reserves leads to increased reproduction and sublegal abundance. Although this is probably true for some species, it can not be the case in our study because reserves were younger than the time required for lobsters to increase in abundance inside reserves and produce offspring that grew to sublegal sizes that I trapped (Kay, *unpublished data*), and because larvae of *P. interruptus* have a planktonic period of 8-10 months and are advected far from parental sites by ocean currents (Johnson 1960, Pringle 1986).

The importance of sampling for fine scale habitat features is suggested by variation in these features among sites (Fig. 4) and the fact that dens (and to a lesser extent, caves and linear crack) significantly influenced response variables in most models (Tables 1 and 2). At all three reserves (Gull, Scorpion, or Carrington) sites closest to the center generally had higher den density than sites immediately inside borders (Fig. 4A). This condition was predicted by our collaborative fishery partners, who correctly anticipated that such fine scale habitat differences would influence trapping dynamics. Among reserve studies that measure or control for habitat effects, habitat is often defined as broad categories (e.g., rocky reef, sand, seagrass meadows) with some measure of topographic relief (Grigg 1994, Stelzenmüller et al. 2007, Forcada et al. 2009). Our results support previous observations that fine scale structural features within such broader habitats (here, the number of dens within rocky reef) can modify catch or abundance (Chapman and Kramer 1999, Harmelin-Vivien et al. 2008). This may be especially true for spiny lobster species that show strong affinities for specific habitat features (Eggleston and Dahlgren 2001, Mai and Hovel 2007). Although measurements of fine scale habitat features are often prohibitively expensive or logistically difficult, considering this level of detail in spatial planning and assessment may improve and inform area based management schemes. The combination of SCUBA habitat surveys and patterns of sublegal abundance provide a level of habitat control that is absent from studies that estimate effects of reserves (and antithetically, fishing) on target species.

Several interesting relationships between catch and the distance of trapping sites from reserve borders emerge from our analyses. First, the decline in the number of lobsters trapped as one moves from the center of reserves towards borders (at sites inside reserves), and from borders further into fished areas, is indicative of net emigration of adults from reserves (*spillover*) as described by theory (Hilborn et al. 2006, Moffitt et al. 2009) and empirical data (McClanahan and Mangi 2000, Kaunda-Arara and Rose 2004, Goñi et al. 2006). This result suggests that some degree of spillover is occurring at the Santa Barbara Channel Islands (SBCI) reserves. Kay et al (*in press*) did not detect spillover with a study design that compared trap yield and recapture of tagged lobsters at multiple sites outside reserves and mean values from sites inside reserve borders. This suggests that detection of gradients via spatially explicit sampling inside reserves may be a more sensitive measure of spillover from reserves, since emigration my not always be detectable in fisheries catches outside reserves. Indeed, spillover of lobsters at SBCI appears to have much less of an impact on fishery catch and effort than in other lobster fisheries (e.g., Goñi et al. 2006, 2010), as suggested by the nonsignificant coefficient value relating catch outside and distance from borders (Table 1, Model [2], *outdist*), and the fact that lobster fishermen at SBCI do not concentrate effort at reserve borders (Kay et al. *in press*).

Another important finding from our study is that the relationship between distance of trapping sites from reserve borders (hereafter: *border distance*) and the number of lobsters caught per trap is relatively steep (and statistically significant) for sites inside but much less steep and not significant outside reserves (Fig. 3A; Table 1, Model [2]). This difference is noteworthy because spillover-mediated changes in catch and/or abundance across reserve borders are commonly described with single functions (linear and non-linear) fitted to data from all sites inside and outside a given reserve (Chapman and Kramer 1999, Kaunda-Arara and Rose 2004, Abesamis et al. 2006, Halpern et al. 2010). The pattern I observed indicates that spillover-mediated catch gradients may not be accurately described by a single function, and it is more similar to piecewise theoretical predictions of Kellner et al. (2007). Interestingly, Kellner et al. predicted that such differences can be caused by fishing the line, a behavior that was absent at our study sites (Kay et al. *in press*). A potential explanation is that over time spillover alone resulted in a relatively steep value for *indist*, but moderate annual harvest rates at SBCI (Kay et al. *in press*) precluded the buildup of lobsters immediately outside reserves.

The catch-border distance patterns I observed provide valuable information about reserves as tools for conservation and fisheries management. From a conservation standpoint, catch-border distance patterns indicate that refuge from fishing mortality is not spatially uniform inside reserves. Rather, fishery-marine reserve interactions (i.e., spillover) at SBCI likely cause low level fishing mortality inside reserves that is highest near borders and declines towards reserve centers. Preliminary results of a collaborative tag-recapture program at our study reserves support this conclusion. Specifically, lobsters tagged by scientists inside reserves and later recaptured by commercial fishermen during fishing operations showed and inverse relationship between the distance of sites inside reserve borders and the proportion of animals that were later captured in the fishery outside reserves (Fig. 5). This spatially differential catch pattern supports the theoretical predictions of spillover (Hilborn et al. 2006). Despite apparent spillover, the average effect of reserve protection was robust and resulted in increased numbers and mean size of lobsters per trap (Figs. 2A and C; Table 1), even for populations near reserve borders (Figs. 3A and C). The extent to which spillover compensates for lost revenue do to Channel Island reserves is unknown and likely to be negligible at present (Guenther 2010), but may increase in the future and is an area of need for continued research (Kay et al., *in press*).

Catch-border distance patterns impact two specific applications of reserves as fishery management tools. First, reserves are emerging as a tool for reference-based stock assessments that use protected populations as proxies for unfished conditions (Morgan et al. 2000, Willis and Millar 2005, Wilson et al. 2010). Second, the biomass that is protected inside reserves is widely cited as a tool that buffers against stock decline or environmental stochasticity, but fishery scientists are only recently addressing the challenge of incorporating the protected biomass into stock assessments (Field et al. 2006). To limit bias in these two applications of marine reserves for stock assessment, it is imperative to measure representative population structures (for reference-based assessments) and the true proportion of a stock that is protected inside reserves (for stock estimates that include protected segments). Here, I provide a quantitative estimate of how organism size and abundance is likely to change relative to location inside marine reserves.

The success of new resource management schemes must be addressed with appropriate science and monitoring, and simply changing management tactics without adequate capacity for assessment is an unlikely formula for success. With regard to area-based management strategies, fundamental considerations include spatially explicit responses of populations and fisheries. This study features an analytical approach for considering and controlling for two important spatial variables (habitat structure and distance from reserve borders) that can inform the implementation and assessment of reserves. Our spatially explicit integration of visual surveys and fishery relevant metrics, as well as the use of sublegal animals to control for habitat effects, are unique in the marine reserve literature. Detailed spatial measurements not only enhance assessments, but may help optimize the design of management strategies as human pressures on marine resources continue to increase globally.

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LITERATURE CITED

Abesamis, R., G. Russ, and A. Alcala. 2006. Gradients of abundance of fish across no-take marine reserve boundaries: evidence from Philippine coral reefs. Aquatic Conservation: Marine and Freshwater Ecosystems 16:349-371.

Agardy, T., P. Bridgewater, M. Crosby, J. Day, P. Dayton, R. Kenchington, D. Laffoley, P. McConney, P. Murray, J. Parks, and L. Peau. 2003. Dangerous targets? Unresolved issues and ideological clashes around marine protected areas. Aquatic Conservation: Marine and Freshwater Ecosystems 13:353-367.

CDFG. 2008. Channel Islands Marine Protected Areas: First 5 Years of Monitoring: 2003-2008. California Department of Fish and Game: (www.dfg.ca.gov/marine)

Chapman, M., and D. Kramer. 1999. Gradients in coral reef fish density and size across the Barbados Marine Reserve boundary: effects of reserve protection and habitat characteristics. Marine Ecology Progress Series 181:81-96.

Côté, I., I. Mosqueira, and J. Reynolds. 2001. Effects of marine reserve characteristics on the protection of fish populations: a meta analysis. Journal of Fish Biology 59 Supplement A:178-189.

DiNardo, G., E. DeMartini, and W. Haight. 2002. Estimates of lobster-handling mortality associated with the Northwestern Hawaiian Islands lobster-trap fishery. Fisheries Bulletin 100:128-134.

Eggleston, D., and C. Dahlgren. 2001. Distribution and abundance of Caribbean spiny lobsters in the Key West National Wildlife Refuge: relationship to habitat features and impact of an intensive recreational fishery. Marine and Freshwater Research 52:1567-76.

Field, J., A. Punt, R. Methot, and C. Thomson. 2006. Does MPA mean 'Major Problem for Assessments'? Considering the consequences of place-based management systems. Fish and Fisheries 7:284-302.

Forcada, A., C. Valle, P. Bonhomme, G. Criquet, G. Cadiou, P. Lenfant, and J. Sánchez-Lizaso. 2009. Effects of habitat on spillover from marine protected areas to artisinal fisheries. Marine Ecology Progress Series 379:197-211.

Friedlander, A., E. Brown, and M. Monaco. 2007. Coupling ecology and GIS to evaluate efficacy of marine protected areas in Hawaii. Ecological Applications 17:715-730.

García-Charton, J., and A. Pérez-Ruzafa. 1999. Ecological heterogeneity and the evaluation of the effects of marine reserves. Fisheries Research 42:1-20.

Goñi, R., S. Adlerstein, D. Alvarez-Berastegui, A. Forcada, O. Reñones, G. Criquet, S. Polti, G. Cadiou, C. Valle, P. Lenfant, P. Bonhomme, A. Pérez-Ruzafa, J. Sánchez-Lizaso, J. García-Charton, G. Bernard, V. Stelzenmüller, and S. Planes. 2008. Spillover from six western Mediterranean marine protected areas: evidence from artisinal fisheries. Marine Ecology Progress Series 366:159-174.

Goñi, R., R. Hilborn, D. Díaz, S. Mallol, and S. Alderstein. 2010. Net contribution of spillover from a marine reserve to fishery catches. Marine Ecology Progress Series 400:233-243.

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 308:207-219.

Gooding, R. 1985. Predation on released spiny lobster, *Panulirus marginatus*, during tests in the northwestern Hawaiian Islands. Marine Fisheries Revue 47:27-35.

Grigg, R. 1994. Effects of sewage discharge, fishing pressure and habitat complexity on coral ecosystems and reef fishes in Hawaii. Marine Ecology Progress Series 103:25-34.

Guenther, C. 2010. A Socio-ecological Analysis of Marine Protected Areas and Commercial Lobster Fishing in the Santa Barbara Channel, California. Ph.D. dissertation. University of California, Santa Barbara.

Halpern, B. 2003. The impact of marine reserves: do reserves work and does reserve size matter? Ecological Applications 13 Supplement:S117-S137.

Halpern, B., S. Lester, and J. Kellner. 2010. Spillover from marine reserves and the replenishment of fished stocks. Environmental Conservation 36:268-276.

Harmelin-Vivien, M., L. Le Diréach, J. Bayle-Sempere, E. Charbonnel, J. García-Charton, D. Ody, A. Pérez-Ruzafa, O. Reñones, P. Sánchez-Jerez, and C.

Valle. 2008. Gradients of abundance and biomass across reserve boundaries in six Mediterranean marine protected areas: Evidence of fish spillover? Biological Conservation 141:1829-1839.

Hartley, T., and R. Robertson. 2009. Stakeholder collaboration in fisheries research: integrating knowledge among fishing leaders and science partners in northern New England. Society & Natural Resources 22:42-55.

Hilborn, R., F. Micheli, and G. De Leo. 2006. Integrating marine protected areas with catch regulation. Canadian Journal of Fisheries and Aquatic Sciences 63:642-649.

Johnson, M. 1960. The offshore drift of larvae of the California spiny lobster, *Panulirus interruptus*. California Cooperative Oceanographic Fisheries Investigations 7:147-161.

Kaunda-Arara, B., and G. Rose. 2004. Effects of marine reef National Parks on fishery CPUE in Coastal Kenya. Biological Conservation 118:1-13.

Kay, M., H. Lenihan, C. Guenther, J. Wilson, C. Miller, and S. Shrout. *In press*. Collaborative assessment of spiny lobster (*Panulirus interruptus*) population and fisheries responses to a marine reserve network. Ecological Applications.

Kay, M., H. Lenihan, C. Miller, and K. Barsky. 2008. Numbers, body size, and movement of lobster. In: Airame S, Ugoretz J (eds) Channel Islands Marine Protected Areas: First 5 Years of Monitoring. Cal Dep Fish Game, Santa Barbara, pp. 8-9.

Kellner, J., I. Tetreault, S. Gaines, and R. Nisbet. 2007. Fishing the line near marine reserves in single and multispecies fisheries. Ecological Applications 17:1039-1054.

Lester, S., B. Halpern, K. Grorud-Colvert, J. Lubchenco, B. Ruttenberg, S. Gaines, S. Airame, and R. Warner. 2009. Biological effects within no-take marine reserves: a global synthesis. Marine Ecology Progress Series 384:33-46.

MacCall, A. 1990. Dynamic Geography of Marine Fish Populations. Washington Sea Grant, Seattle

Mai, T., and K. Hovel. 2007. Influence of local-scale and landscape-scale habitat characteristics on California spiny lobster (*Panulirus interruptus*) abundance and survival. Marine and Freshwater Research 58:419-428.

McClanahan, T., and S. Mangi. 2000. Spillover of exploitable fishes from a marine park and its effects on the adjacent fishery. Ecological Applications 10:1792-1805.

Moffitt, E., L. Botsford, D. Kaplan, and M. O'Farrell. 2009. Marine reserve networks for species that move within a home range. Ecological Applications19:1835-1847.

Morgan, L., L. Botsford, S. Wing, and B. Smith. 2000. Spatial variability in growth and mortality of the red sea urchin, *Strongylocentrotus franciscanus*, in northern California. Canadian Journal of Fisheries and Aquatic Sciences 57:980-992.

Prince, J. 2005. Combating the Tyranny of Scale for haliotids: Micro-management for Microstocks. Bulletin of Marine Science 76:557-578.

Pringle, J. 1986. California spiny lobster (*Panulirus interruptus*) larval retention and recruitment: A review and synthesis. Canadian Journal of Fisheries and Aquatic Sciences 43:2142-2152.

Rakitin, A., and D. Kramer. 1996. Effect of a marine reserve on the distribution of coral reef fishes in Barbados. Marine Ecology Progress Series 131:97-113.

Sale, P., R. Cowen, B. Danilowicz, G. Jones, J. Kritzer, K. Lindeman, S. Planes, N. Polunin, G. Russ, Y. Sadovy, and R. Steneck. 2005. Critical science gaps impede use of no-take fishery reserves. Trends in Ecology and Evolution 20:74-80.

Stelzenmüller, V., F. Maynou, and P. Martin. 2007. Spatial assessment of benefits of a coastal Mediterranean marine protected area. Biological Conservation 136:571-583.

UNEP-WCMC. 2008. National and Regional Networks of Marine Protected Areas: A Review of Progress. United Nations Environment Programme World Conservation Monitoring Centre, Cambridge.

Willis, T., and R. Millar. 2005. Using marine reserves to estimate fishing mortality. Ecology Letters 8:47-52.

Wilson, J., J. Prince, and H. Lenihan. 2010. A management strategy for sedentary nearshore species that uses marine protected areas as a reference. Marine and Coastal Fisheries: Dynamics, Management and Ecosystem Science 2:14-27.

Table 2.1. Results of multiple linear regression models for the influence of experimental and environmental factors (predictor variables) on three response variables: (a) number of legal sized lobsters; (b) number of sublegal lobsters, and; (c) the mean size of legal lobsters that were captured in traps. The response variables for each model are listed (in italics) in the top row, and the predictor variables are listed in the first column. Model (1) compares trapping data at sites categorically inside versus outside reserves, whereas Models (2) and (3) estimate spatially explicit linear (Model 2) and nonlinear (Model 3) responses (see *Materials and Methods*). Values reported for each predictor variable include the coefficient, the t-statistic robust to heteroscedasticity (in parentheses), and the level at which statistical significance was detected (one, two, and three asterisks to indicate statistical significance at the 0.05, 0.01, and 0.001 levels, respectively).

	Model 1			Model 2			Model 3		
	# legals	*# sublegals*	*mean size legals*	*# legals*	*# sublegals*	*mean size legals*	*# legals*	*# sublegals*	*mean size legals*
Reserve	__5.49(8.90)***__	__0.92(3.45)**__	__6.77(6.24)***__	---	---	---	---	---	---
indist	---	---	---	__2.99(9.84)***__	__0.78(4.78)***__	1.09(1.30)	2.27(1.30)	0.98(1.18)	3.56(1.85)
$(\text{indist})^2$	---	---	---	---	---	---	0.07(0.21)	-0.03(-0.18)	-0.98(-2.11)
outdist	---	---	---	-0.24(-0.92)	0.21(1.55)	__-1.53(-3.18)**__	-1.92(-1.21)	0.57(0.76)	__-5.39(-3.47)**__
$(\text{outdist})^2$	---	---	---	---	---	---	0.28(1.23)	-0.06(-0.56)	__0.80(3.33)**__
Depth	-0.01 (-1.02)	-0.02(-2.02)	0.03(1.58)	-0.02(-1.69)	__-0.02(-2.16)*__	0.04(1.44)	-0.02(-1.51)	__-0.02(-2.18)*__	0.04(1.62)
Nights	__0.18(2.62)*__	__0.21(6.91)***__	-0.09(-1.03)	__0.18(2.48)*__	__0.21(6.68)***__	-0.10(-1.09)	__0.18(2.48)*__	__0.21(6.65)***__	-0.11(-1.22)
Dens	__0.22(3.71)**__	0.02(0.63)	__0.21(2.27)*__	__0.07(2.38)*__	-0.03(-0.91)	__0.28(2.75)*__	0.13(1.47)	-0.05(-0.82)	__0.29(3.43)**__
Caves	__0.77(3.29)**__	0.18(1.52)	-1.05(-1.75)	0.17(0.69)	0.10 (0.81)	__-2.16(-3.77)**__	0.30(1.04)	0.08(0.64)	__-1.16(-3.39)**__
Cracks	0.01(0.24)	0.02(1.72)	__0.07(2.30)*__	-0.01(-0.15)	-0.01(-0.64)	0.15(1.41)	0.04(0.66)	-0.02(-0.70)	0.18(1.92)
Scorpion	__-8.55(-6.38)***__	-1.97(-2.08)	1.46(1.11)	__-3.88(-2.35)*__	-0.36(-0.39)	1.61(1.01)	__-5.06(-2.29)__	-0.10(-0.08)	0.58(0.34)
Carrington	-0.74(-.055)	-0.7.3(-1.21)	__2.33(2.46)*__	-0.29(-0.22)	-0.14(-0.23)	0.66(0.31)	-0.67(-0.50)	-0.08(-0.05)	2.04(1.08)
Gull	--	--	--	--	--	--	--	--	--
2006	-2.89 (-2.15)	__-1.88(-2.67)*__	2.42(1.99)	-2.26(-1.89)	__-1.75(-2.39)*__	__3.02(2.82)*__	-2.33(-2.00)	__-1.74(-2.39)*__	__2.84(2.40)*__
2007	0.09 (0.20)	-0.66(-1.55)	-0.04(-0.07)	0.08(0.16)	-0.68(-1.50)	0.15(0.29)	0.09(0.18)	-0.68(-1.50)	0.16(0.32)
2008	--	--	--	--	--	--	--	--	--
Constant	__-8.89(4.08)***__	0.02(0.02)	__89.11(67.31)***__	2.29(1.44)	__2.39(4.54)***__	__92.94(59.89)***__	2.20(1.59)	__2.40(4.27)***__	__91.79(125.20)***__
Obs.	1955	1955	1442	1955	1955	1442	1955	1955	1442
Adj. R^2	0.36	0.08	0.20	0.39	0.09	0.17	0.39	0.09	0.21

Table 2.2. Results of multiple linear regression models (1, 2, and 3) reported in Table 1, but for which the number of sublegal lobsters in each trap is used as a predictor variable. The rationale is that sublegals are ecologically similar to adults, but are not directly removed through fishing, and therefore provide an additional control for the effect of habitat on the number and mean size of legal lobsters in traps. Values reported for each predictor variable include the coefficient, the t-statistic robust to heteroscedasticity (in parentheses), and the level at which statistical significance was detected (one, two, and three asterisks to indicate statistical significance at the0.05, 0.01, and 0.001 levels, respectively).

	Model 1		Model 2		Model 3	
	# legals	*mean size legals*	*# legals*	*mean size legals*	*# legals*	*mean size legals*
Reserve	**4.81(9.30)*****	**7.03(7.23)*****	---	---	---	---
indist	---	---	**2.43(7.64)*****	1.35(1.67)	1.56(1.07)	3.77(2.13)
$(\text{indist})^2$	---	---	---	---	-0.10 (0.31)	**-0.97(-2.22)***
outdist	---	---	-0.40(-1.69)	**-1.41(-3.15)****	-2.33(-1.87)	**-5.25(-3.43)****
$(\text{outdist})^2$	---	---	---	---	0.33(1.82)	**0.80 (3.33)****
# sublegals	**0.74(3.62)****	**-0.37(-3.67)****	**0.72(3.76)****	**-0.34(-3.66)****	**0.73(3.75)****	**-0.33(-3.48)****
Depth	0.003 (0.62)	0.03(1.51)	-0.003(-0.67)	0.03(1.36)	-0.001(-0.20)	0.03(1.53)
Nights	0.03(0.56)	-0.01(-0.15)	0.03(0.47)	-0.03(-0.31)	0.27(0.49)	-0.04(-0.46)
Dens	**0.20(4.56)*****	**0.21(2.78)***	**0.10(3.36)****	**0.26(2.81)***	**0.16(2.76)***	**0.27(3.67)****
Caves	**0.63(2.33)***	-0.97(-1.80)	0.10(0.38)	**-2.10(-3.95)****	0.24(0.99)	**-1.11(-3.37)****
Cracks	-0.01(-0.15)	**0.07(2.68)***	0.002(0.07)	0.14(1.40)	0.05(1.05)	0.18(1.92)
Scorpion	**-7.09(-6.57)*****	0.78(0.75)	**-3.62(-2.31)***	1.56(1.05)	**-4.98(-2.91)***	0.54(0.33)
Carrington	-0.20(-0.18)	**2.01(2.54)***	-0.19(-0.18)	0.59(0.29)	-0.64(-0.58)	1.96(1.08)
Gull	---	---	---	---	---	---
2006	-1.49(-1.24)	1.68(1.52)	-0.99(-0.95)	**2.39(2.35)***	-1.06(-1.02)	**2.23(2.00)***
2007	0.58 (1.19)	-0.30(-0.53)	0.60(1.19)	-0.10(-0.17)	0.58(1.24)	-0.09(-0.17)
2008	---	---	---	---	---	---
Constant	-1.82(-1.66)	**90.09(73.19)*****	0.57(0.47)	**93.97(58.53)*****	0.46(0.44)	**92.81(122.05)*****
Observations	1955	1442	1955	1442	1955	1442
Adj. R^2	0.51	0.22	0.53	0.19	0.53	0.22

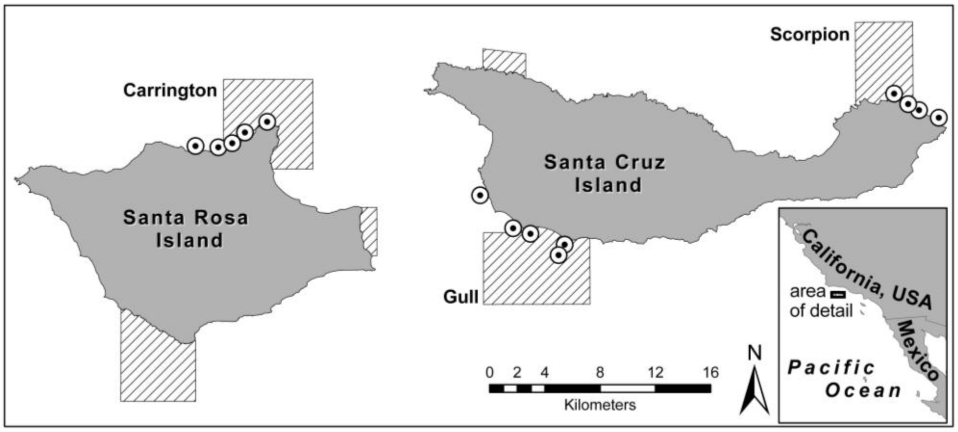

Figure 2.1. Map of Santa Cruz and Santa Rosa Islands in the Southern California Bight (inset), including the sites at Carrington, Gull, and Scorpion reserves where collaborative trapping and SCUBA habitat surveys took place (black dots).

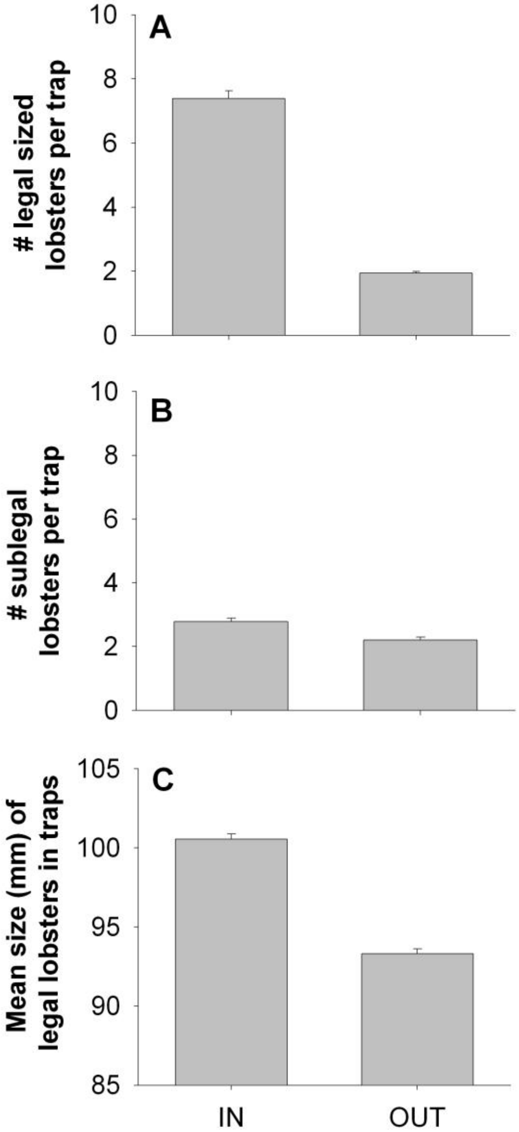

Figure 2.2. Mean number of legal sized (≥82.5 mm carapace length) lobsters (A) and sublegal lobsters (B), and the mean size (C) of all legal sized lobsters (±SE) caught in traps inside versus outside the Carrington, Gull, and Scorpion MPAs.

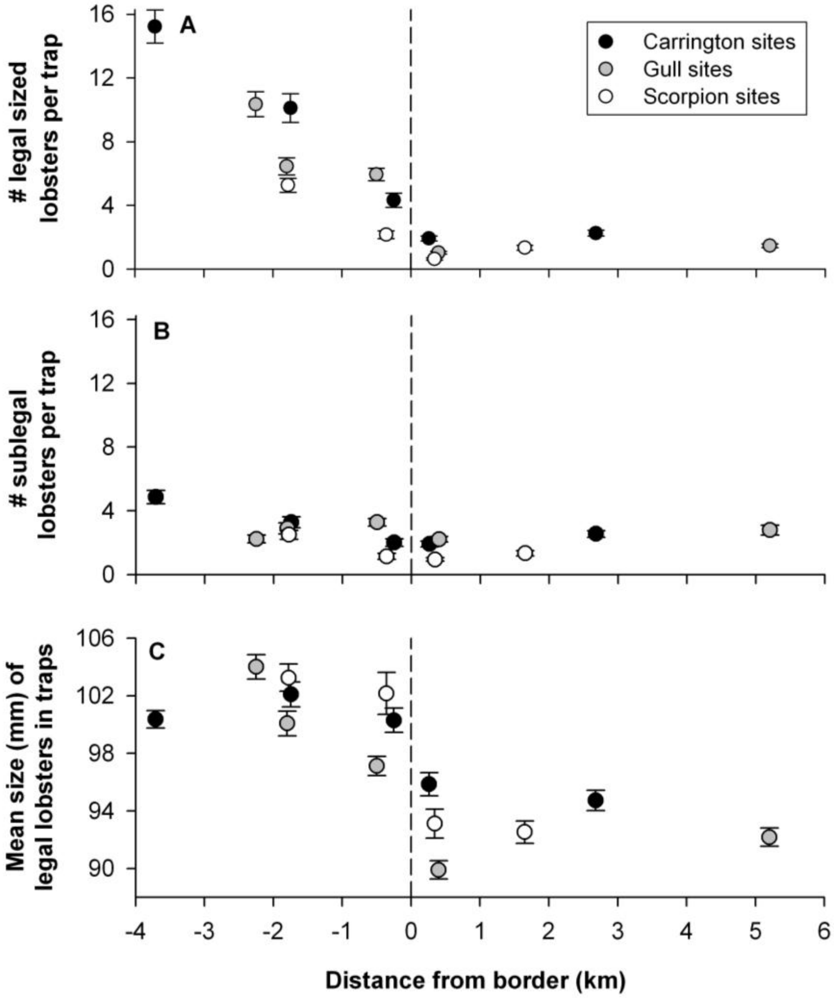

Figure 2.3. Mean number of legal sized (≥82.5 mm carapace length) lobsters (A) and sublegal lobsters (B), and the mean size (C) of all legal sized lobsters (±SE) trapped at sites associated with the Carrington, Gull, and Scorpion MPAs, and the distance of each site from the nearest reserve border (vertical dashed lines).

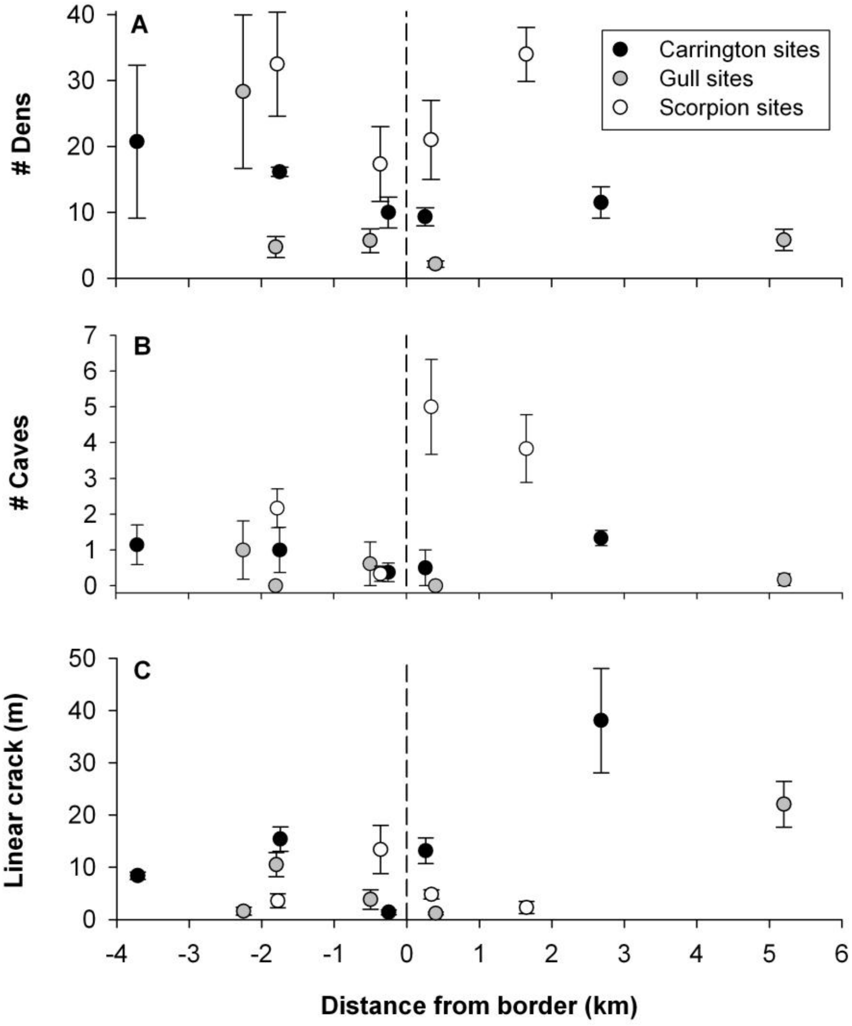

Figure 2.4. The number of dens (A), caves (B), and the linear extent (in meters) of crack (C) recorded on rocky reef trapping sites (±SE). Data were collected with SCUBA, means are from six to eight replicate 450m^2 transects at each site.

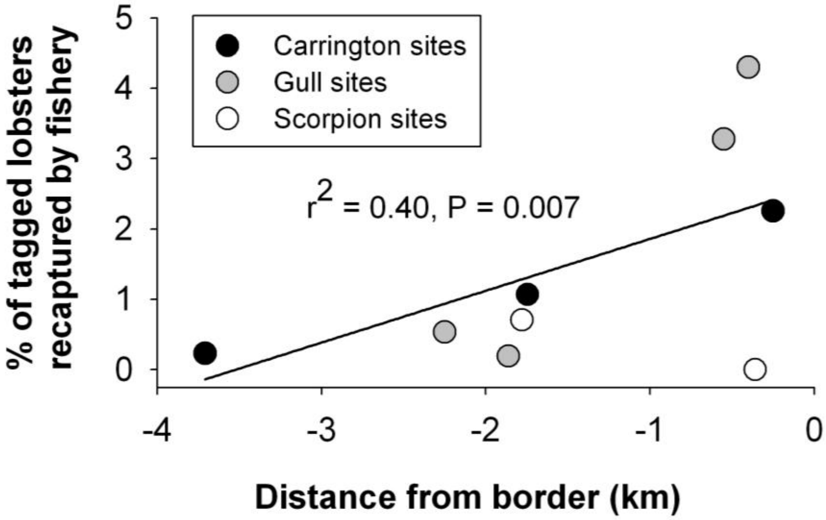

Figure 5. The percentage of tagged lobsters, at each site inside reserves, that were later recaptured and reported by fishermen outside reserves.

CHAPTER 3

Spatially Explicit Mortality of California Spiny Lobster (*Panulirus interruptus*) Across a Marine Reserve Network

INTRODUCTION

Benefits of marine reserves for conservation and fisheries management are predicated upon reduced mortality for target organisms inside reserves. Interestingly however, very few studies describe how reserves influence mortality rates (but see Attwood 2003; Willis and Millar 2005; Götz et al. 2008; Taylor and McIlwain 2010). Empirical studies of marine reserves focus on differences in organism density, abundance, and size inside versus outside reserves (reviews by Côté et al. 2001; Halpern 2003; Lester et al. 2009), which is sensible because a common objective of conservation is to increase these attributes for depleted populations. Understanding changes in mortality across space in relation to reserve protection is a critical component of evaluating not only the conservation benefit of reserves, but also the contribution of reserves to fisheries management objectives.

Two important fisheries benefits of marine reserves are enhanced by understanding how reserves affect mortality rates of harvested species. The first is the use of populations inside reserves as references for unfished populations (Babcock and MacCall 2010, McGilliard et al. 2010, Wilson et al. 2010) or for estimating life history parameters used in fishery assessments (Bohnsack 1999, MacPherson et al. 2000; Taylor and McIlwain 2010, Wilson 2011). A key example of the latter involves estimates of natural mortality (*M*), which is an essential parameter for many fisheries models (Hilborn and Walters 1992), but is difficult to measure in part because it is confounded by fishing activity in harvested areas outside reserves (Willis and Millar 2005). The second benefit relates to potential increases in fishery yield due to larval export, which results from increased lifetime egg production (LEP) of older, larger, and more abundant organisms inside reserves, and the subsequent redistribution of this reproductive output to nearby fished areas (Botsford et al. 2009). Estimation of reserve-based increases in LEP and fisheries yield is typically based upon individual or population level models that employ estimates of natural and fishing mortality (Beverton and Holt 1957; Guénette et al. 1998). Consequently, a spatially explicit understanding of how reserves influence mortality is fundamental to understanding if and how reserves can influence LEP and fishery yield.

An additional mechanism by which reserves can benefit fisheries is the net emigration of adults from within reserves to fished areas (*spillover*). Models of spillover consistently predict that increases in organism abundance and/or biomass inside reserves are lowest near reserve borders because the likelihood of emigration increases near borders, regardless of whether movement is driven by 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). Empirical support for these predictions is mixed (Chapman and Kramer 1999, Kaunda-Arara and Rose 2004, Abesamis et al. 2006, Goñi et al. 2006, Harmelin-Vivien et al. 2008), and clear gradients predicted by models are undoubtedly obscured by spatially heterogeneous habitat and ecological processes (García-Charton and Pérez-Ruzafa 1999). Where present, such gradients might indicate differential mortality inside reserves due to spillover, but no studies have explored changes in mortality as a function of distance from reserve borders. Understanding the magnitude and spatial extent of spillover-mediated fishing mortality inside reserves presents a critical challenge for accurate estimates of biomass or LEP of reserve populations, and for selecting assessment reference sites inside reserves that are not (or are minimally) impacted by spillover.

In this study I examine how mortality rates for a target organism vary among sites throughout a reserve network, and I test two specific predictions: (1) mortality rates are lower inside versus outside reserves, and; (2) mortality inside reserves is highest near borders and declines towards reserve centers. To test these hypotheses, I measured mortality rates for California spiny lobster (*Panulirus interruptus*) on reefs located at varying distances inside and outside borders of three reserves at the Santa Barbara Channel Islands (SBCI) in California, USA. Previous work with *P. interruptus* at the SBCI reserve network demonstrates robust population increases inside reserves (Kay et al. *In press*) as well as abundance gradients inside reserves that are most likely due to spillover (Kay, unpublished data). Consequently, this system presents an ideal opportunity to examine how mortality rates vary across space inside and outside of marine reserves. This study is the first to describe spatially explicit and empirical estimates of mortality across multiple reserves in a network.

MATERIALS AND METHODS

Site selection and sampling

We estimated mortality rates of female California spiny lobster (*Panulirus interruptus*) populations on 16 reefs inside and outside of three marine reserves at the Santa Barbara Channel Islands (SBCI), California, USA (Fig. 1). General characteristics of the SBCI marine reserve network (CDFG 2008), as well as the selection process for sites used in this study, are described elsewhere (Kay et al. *In press*). Briefly, scientists and commercial lobster fishermen worked collaboratively to identify reefs with similar physical, ecological, oceanographic, and fishery catch (prior to reserve implementation) characteristics. I sampled six reefs inside or nearby (<6 km) the Carrington (Santa Rosa Island) and Gull Island (Santa Cruz Island) marine reserves, and I sampled four reefs associated with the Scorpion marine reserve off of Santa Cruz Island (total number of reefs sampled = 6 + 6 + 4 = 16 total). I used GIS (ArcGIS 9.3.1, ESRI) to calculate the distance of the midpoint of each sampling area to the nearest reserve border.

We sampled spiny lobster length frequency distributions at each reef using 10-15 replicate lobster traps that were sampled every 1-4 days from August-December 2007 and 2008. Traps were identical to those used in the fishery for *P.*

interruptus at SBCI and are described in detail in Kay et al. (*In press*). Traps were deployed in a stratified haphazard array at each reef and were sampled from either commercial fishing vessels or a research vessel equipped with a commercial-grade trap hauler. As each trap was retrieved I recorded the sex and carapace length (nearest mm using vernier calipers) of all lobsters in the trap. Additionally, lobsters were tagged with an individually numbered T-bar tag (TBA-2 standard, Hallprint Tags, Australia) 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. I minimized stress to lobsters on deck by covering them with wet burlap sacks, placing them in standing seawater, and returning them to the ocean as quickly as possible. After lobsters had been processed, they were returned to the exact location of capture (using GPS coordinates) and released by hand.

Statistical approach

We estimated mortality rates of female lobsters on each reef using a length-based linearized catch curve (LCC) analysis that is described in detail by Sparre and Venema (1998, Chapter 4). The LCC employs two types of data: (1) length frequency data, described above, and; (2) estimates for parameters of the Von Bertalanffy growth function (VBGF; Eq. [1]):

$$L_t = L_\infty\left(1 - \exp\left(-K\left(t - t_0\right)\right)\right) \tag{1}$$

where L_t is the length of individuals at age t; L_∞ is the mean asymptotic length; K is the growth rate; and t_0 is the theoretical age at which length is zero. I estimated these parameters from lobsters that were tagged and recaptured over a three year period from 2006-2009 at our field sites (Fig. 1). VBGF parameters were estimated using an expression of the VBGF that is explicitly designed for use with tag-recapture data where length at initial tagging, the length at recapture, and time elapsed between tagging and recapture are used to estimate L_∞ and K (Quinn and Deriso 1999). This expression takes the following form (Eq. [2]):

$$\Delta L_j = (L_\infty - L_{ij})(1 - e^{-K\Delta tj}) \tag{2}$$

where ΔL_j is the change in length (growth increment) between tagging and recapture for individual lobster j; L_{ij} is the initial length of lobster j at tagging; Δtj is the time elapsed between initial tagging and recapture for individual j; and L_∞ and K are free parameters estimated by the model.

Several aspects of recapture data used to estimate L_∞ and K warrant mention: (1) t_0 is not estimable from tag-recapture data alone and by convention I assume $t_0 =$ zero; (2) reliable estimates for L_∞ and K were not obtained for male lobsters because annual growth increments for the largest males I tagged and recaptured were as high as the maximum annual values I observed at any size class, and therefore I were not able to reliably estimate L_∞ (the mean asymptotic size). Rather than assuming equal growth for both sexes, or forcing a value for male L_∞, I opted for a more conservative approach and proceeded with an analysis that considers growth and mortality for female lobsters only; (3) recapture data were pooled from all sites in our study; (4) I fit Eq. (2) to lobsters that were captured within 3 weeks of the anniversary of their tagging in order to minimize bias that results from seasonal and incremental growth over very short time intervals or during time periods that do not include all annual seasons. This required a large number of individual lobsters to be tagged, and the analysis here employed 481 females recaptured from the ~9756 females tagged; (5) I used data only from lobsters that were tagged and recaptured inside reserves in order to avoid underestimates of *K* due to differential harvest of fast growing individuals, and underestimates for L_∞ due to truncated size structure of fished populations.

Once VBGF parameters were estimated, a LCC was analyzed as described by Sparre and Venema (1998). The first step was to convert our length frequency size classes (1 mm bins) into age classes. This was accomplished by entering our VBGF parameter estimates from Eq. (2) into the inverse Von Bertalanffy equation (Eq. [3]):

$$Age_L = t_0 - \frac{1}{K} * \ln\left(1 - \frac{L}{L_\infty}\right) \tag{3}$$

where Age_L is the age of lobsters at individual size class *L* (here, 1 mm bins); and t_0, *K*, and L_∞ are as described above. Next, the proportion of lobsters in each age class in the observed data (i.e., length frequencies converted to age classes via Eq. [3]) was adjusted using the following equation:

$$Nadj_a = \ln\left(\frac{N_a}{\Delta t_a}\right) \tag{4}$$

where $Nadj_a$ is the adjusted proportion of lobsters at age a; N_a is the proportion of lobsters in age class a from the observed length frequency data (converted to age classes); and Δt_a is amount of time that a lobster with average growth spends in age class a (estimated directly from results of equation 3).

These two steps (Eqs. [3] and [4]) yield a linear relationship between $Nadj_a$ (the y axis variable; hereafter referred to as *ln frequency*) and each age class (the x axis variable), to which a least squares linear regression can be fit (Eq. [5]):

$$Nadj_a = X_a Z + b \tag{5}$$

where $Nadj_a$ (*ln frequency*) is the adjusted number of lobsters in each age class a; X_a represents each age class a; Z is the slope of the regression line; and b is the y-intercept. The parameter of interest in this regression is Z, whose negative value is the mortality rate. Data for each of our sampling sites (Fig. 1) were plotted separately and Eq. (5) was fitted to data for each site. The age class in which the greatest percentage of lobsters was captured represents age at which animals are fully selected by fishing gear, and Eq. (5) was not fitted to data points to the left of this peak. Finally, in order to measure the effect of marine reserves on mortality rates, Eq. (5) was fitted only to age classes not exposed to fishing pressure prior to reserve implementation in April 2003 (i.e., age classes above the legal size limit prior to April 2003 were excluded from LCC analyses at all sites).

We characterized uncertainty in our VBGF parameter estimates by fitting Eq. (2) to 1000 bootstrapped subsamples (with replacement) of our tag-recapture data. Similarly, uncertainty in our length frequency data was characterized by bootstrapping (with replacement) 1000 individual subsamples of the observed data. Individual estimates of L_∞ and K were then interacted with individual length frequency subsamples (Eq. [3]) to produce 1000 unique arrays of age classes. I then applied Eqs. (4) and (5) to each of these unique arrays such that I ultimately attained 1000 estimates of Z (mortality) at each site. The mean (±SD) of these 1000 estimates are reported for each of our 16 sites inside and outside reserves.

Mean estimates of spiny lobster mortality (Z) at our 16 sites were used in linear regression analyses to examine spatial differences in mortality across the Santa Barbara Channel Islands reserve network. To test the hypothesis that reserves decrease mortality for populations within their borders, I specified the following regression model:

$$Y = \alpha + \beta In\_reserve + \gamma Scorpion + \delta Carrington + \varepsilon \qquad (6)$$

where response variable Y is the mortality (Z) I estimated at our sites; α is the intercept (constant); *In_reserve* is a categorical variable indicating sites inside any reserve; and *Scorpion* and *Carrington* are categorical variables for sites associated with the Scorpion and Carrington reserves, with Gull as the omitted category. Coefficient β describes the influence of the *In_reserve* predictor variable (i.e., location inside vs. outside any of the three reserves) on the response variable; coefficients γ and δ account for the average differences in response variables by reserve using Gull as the basis for comparison; and ε is the error term (variance not explained by the model).

To test the hypothesis that mean mortality rates at each site change depending upon distance from marine reserve borders, I specified the following model:

$$Y = \alpha + \beta_1 \mathit{Distance\_in} + \beta_2 \mathit{Distance\_out} + \varphi \mathit{Gull} + \delta \mathit{Carrington} + \varepsilon \quad (7)$$

where Y is the mortality I estimated at our sites; *Distance_in* and *Distance_out* are continuous variables and are vectors of distances of individual trapping sites inside or outside the nearest reserve border, respectively (for sites inside borders, *Distance_out* values were set to zero, and for sites outside borders, *Distance_in* values were set to zero); and *Gull* and *Carrington* are categorical variables for sites associated with the Gull and Carrington reserves, with Scorpion as the omitted category.. Coefficients β_1 and β_2 describe the influence of *Distance_in* and *Distance_out* on the response variable; coefficients φ and δ account for the average differences in response variables by reserve using Scorpion as the basis for comparison; and α and ε are as described above. Regression models were specified to be robust to heterogeneity of variance and were estimated using STATA 9 (StataCorp, 2005). Statistical significance was determined at the 0.05 level.

RESULTS

Length frequency data at the innermost Carrington reserve site (Carrington Point, 3700 m from nearest border) showed a clear mode centered at ~100 mm carapace length (Fig. 2). Among all sites within the Carrington reserve, the height of this mode relative to smaller size classes became progressively smaller with proximity to the reserve border. This pattern is reflected in the catch curve mortality estimates at each of these sites, which show a clear relationship between increased mortality and proximity to the border. Specifically, the mortality rates at individual sites ranged from $Z = 0.04$ at Carrington Point, 0.15 at Grassy Knoll (1800 m inside) and 0.49 at the Border site (250 m inside; Fig. 2). Length frequency data at sites outside the Carrington reserve were comprised of fewer large sized lobsters than at sites inside the reserve, and corresponding mortality estimates were higher (ranging between $Z = 0.55$ and 0.56) and much less variable than for sites inside reserves (Fig. 2).

Length frequency data and corresponding mortality estimates for the Scorpion reserve (Fig. 3) indicated important similarities and differences when compared to the Carrington sites. Unlike Carrington, no mode of larger animals was evident in the length frequency data, and mortality estimates for the two sites inside the reserve were both relatively high: $Z = 0.32$ for Cavern Point (1750 m inside) and 0.29 for Scorpion Anchorage (300 m inside). As with the Carrington sites, however, sites outside the reserve had higher mortality than sites inside the reserve: $Z = 0.59$ at Scorpion Anchorage (200 m outside) and 0.55 at Scorpion Far (1650 m outside).

At the Gull Island reserve, length frequency data at the innermost site (Gull Island, 2250 m inside reserve) showed a mode centered on ~103 mm (Fig. 4) that was absent at Punta Arena (1850 m inside), East Morse (300 m inside) and West Morse (150 m inside). Interestingly, catch curve mortality estimates among these sites are highest at Punta Arena ($Z = 0.22$), similar at Gull Island and East Morse ($Z = 0.11$), and intermediate at West Morse Point ($Z = 0.18$). Mortality estimates at sites outside reserves were much higher than inside: $Z = 0.62$ and 0.69 at Morse Point Out (400 m outside border) and Kinton Point (5200 m out), respectively.

The mean mortality rate among the nine sites inside all three reserves was 0.21 (±0.07 SE), but was 0.59 (±0.02 SE) for the seven sites outside reserves, and the difference was highly statistically significant (Fig. 5, Table 1). The coefficient value of $\beta = -0.37$ for Eq. (6) indicates that the average effect of reserves was a Z reduction of 0.37. The relationship between mortality rate and distance from nearest reserve border was significant for sites inside reserves, and the coefficient value $\beta_1=-0.0001$ (Table 1) in Eq. (7) indicates a marginal effect of reserves such that Z was reduced by 0.0001 for every meter moved from reserve borders towards reserve centers. A notable exception to the general pattern was relatively low mortality measured at the East Morse and West Morse sites immediately inside the Gull reserve border.

DISCUSSION

This is the first empirical study in which mortality rates for a fished species are examined across multiple reserves and as a function of distance from reserve borders. Drastically reduced mortality for female lobsters inside reserves across the Santa Barbara Channel Islands (SBCI) network (Fig. 5, Table 1) indicates that these reserves are an effective conservation tool. This reduced mortality is likely the primary driver of increased numbers and sizes of lobsters observed by Kay et al. (*In press*) at the same sites, and linking the two results is important because perceived reserve effects can be confounded by high spatio-temporal variability in marine systems (García-Charton and Pérez-Ruzafa 1999; Willis et al. 2003). Our prediction that mortality inside reserves should be influenced by distance from borders was confirmed statistically, but the only individual reserve to demonstrate the pattern clearly was Carrington. This trend may strengthen over time as lobster abundance and mean size continues to increase inside the relatively young SBCI reserves (Kelly et al. 2000; Shears et al. 2006).

In general, site-specific mortality rates for female lobsters were much less variable outside reserves than inside reserves. Our spatially explicit regression model (Eq. [7]) accounted for 70% of the total variance (Table 1) of Z estimates among sites, and most variability was observed inside reserves. This suggests that spillover-mediated fishing mortality is one of multiple factors that cause highly variable mortality inside reserves.

Variable mortality within reserves has important implications for the use of reserves as fishery management tools. If some fraction of total mortality (Z) experienced by populations immediately inside borders is due to spillover-mediated fishing mortality (F), then sites inside reserves that are used to estimate natural mortality (M) should be located near the interior of reserves. The distance inside reserves at which total mortality is representative of M and not (or very minimally) impacted by F is a function of the relative scales of organism movement and reserve size (Kaunda-Arara and Rose 2004; Moffitt et al. 2009). Tagging studies at the Santa Barbara Channel Islands indicate that nearly 80% of tagged lobsters are recaptured within 2 km of their initial tagging site, and the distance moved is not time-dependent (Kay et al. 2008). This scale of movement is smaller than the width (measured as the linear along-shore distance between borders) of the Carrington (~7.7 km), Gull (~4.7 km of shoreline, but ~7.7 km max width because the reserve extends farther west just offshore – see Fig. 1), and Scorpion (~4.1 km) reserves. Given these relative spatial scales, sites located ~2 km or farther inside reserve borders in this study provide reasonable estimates of M for female lobsters. Among the five sites not immediately inside reserve borders the mean estimate of Z was 0.17 (±0.05 SE). This estimate, and the overall mean estimate from sites within reserves (0.21 [±0.07 SE]), is similar to *M* values estimated for other temperate spiny lobster species (Pollock 1981; Groenveld 2000; Caputi et al. 2008; Haist et al. 2009).

Variable total mortality inside reserves might reflect actual differences in *M*, but additional explanations include dynamic ecological processes between sites/reserves or biases in the models I used. For example, relatively low mortality at the Gull border sites (East and West Morse Point; Figs. 4 and 5), as compared to the Scorpion and Carrington Border sites, may be due to two important physical features. First, sampling at the West and East Morse sites occurred near a prominent rocky reef (Morse Point) that provides high relief habitat, reaches the sea surface even at high tide ~150 m offshore, and has a history (i.e., pre-reserve) of high catches. Furthermore, this feature extends offshore within the reserve for many miles as a deepwater (~50 m deep) ridge, and the local ecological knowledge (LEK; Hartley and Robertson 2009) of fishermen collaborators indicates that this might serve as a seasonal migration corridor. These physical attributes may reduce along-shore movement across the nearest reserve border and into fished areas, which would lower mortality rates of populations at this site. This effect is suggested by lower mortality at East Morse (interior side of Morse point) than at West Morse (border side of Morse Point), even though the two sites are separated by only ~150 m (Fig. 5). No such feature is present at the Carrington Border site, and relatively high *Z* estimates at both Scorpion sites may be due in part to the narrow width (and thus higher emigration) of that reserve. The second physical difference is that the Gull site is south-facing whereas the Scorpion and Carrington reserves face north. This is important because large winter storm swells during the fishing season transmit higher energy to nearshore reefs on the north-facing side of the Channel Islands, and such storm events trigger large scale lobster movements that likely increase emigration rates.

An alternative explanation for lower total mortality measured at the Gull Border sites is that, while M and per capita emigration rates might be the same at all border sites, larger size classes show a behavioral preference for the type of habitat at Gull Border relative to Carrington and Scorpion border sites. This explanation is feasible because commercial and recreational fishermen LEK suggests that lobsters are often distributed heterogeneously based on demography (sex and/or size class) and habitat. This is supported by observations of Kay (*unpublished data*) who found a significant relationship between lobster size and the density of lobster dens across the same sites in this study, and the common observation that small size classes utilize surfgrass (*Phyllospadix spp.*) as a preferred habitat (Engle 1979). Indeed, these ecological relationships might explain perceived mortality rates at Punta Arena ($Z = 0.22$) that were high relative to those at Gull Island ($Z = 0.16$), even though the sites are similar distances from reserve borders. Specifically, a large area at the Punta Arena site is a shallow and low-relief surfgrass meadow, whereas Gull Island has greater structural complexity, higher density of lobster dens (Kay, unpublished data), and a reputation for historically high fishery catches characterized by large lobsters.

Consequently, it is possible that the disparity in *Z* estimates for these two sites is an artifact of bottom-up ecological differences that select for different size classes of lobsters and therefore bias estimates of our length-based model. Although this conclusion is speculative, it underscores the importance of interpreting fisheries models in the local ecological context to which they are applied, and it demonstrates the prudence of estimating *M* from multiple sites near reserve centers.

Low variability in mortality rates (*Z*) among sites outside reserves, as compared to *Z* inside reserves, may be due to spatially heterogeneous fishing effort that is allocated in proportion to the abundance of target organisms. This behavior is predicted by the ideal free distribution (Abrahams and Healy 1990) and is documented under certain circumstances from at least one other crustacean fishery (Swain and Wade 1993). Adherence to the ideal free distribution is variable within and among fisheries (Abernathy et al. 2007), but it is possible that mortality imposed through heterogeneous fishing effort at our sites may have masked the high natural variability in *Z* that was apparent inside reserves.

This study quantifies the conservation value of a reserve network for reducing mortality to female *P. interruptus*. The fact that I detected a significant mortality-distance relationship inside reserves, but mortality was highly variable, demonstrates the need for further empirical study to elucidate spatially explicit mortality patterns inside and outside marine reserves. Ideally, future studies will explore the generality of distance-mortality relationships inside reserves and relate these to known movement rates for multiple species. Increased mortality for populations immediately inside reserve borders indicates a fundamental tradeoff between spillover benefits to adjacent fisheries through increased yield and benefits to fisheries derived from increased LEP or reserve-based assessments. The inherent tradeoff is that spillover effectively connects reserve populations with fished areas, such that some level of fishing mortality is exerted on reserve populations, but LEP and the accuracy of estimates for M are maximized when fishing mortality is absent inside reserves. Linking estimates of mortality inside reserves to rates of spillover and associated yield is an important frontier in marine reserve research, because doing so allows direct comparison of the tradeoffs between spillover (and consequent increased mortality inside reserves) and LEP and the reliability of reserve-based assessments. I demonstrate here that variable mortality inside reserves does not preclude use of reserves in estimating M, but care must be taken in selecting reference sites, especially when ecological heterogeneity can bias models.

LITERATURE CITED

Abernethy, K., E. Allison, P. Molloy, and I. Côté. 2007. Why do fishers fish where they fish? Using the ideal free distribution to understand the behavior of artisanal reef fishers. Canadian Journal of Aquatic and Fisheries Sciences 64: 1595-1604.

Abesamis, R., G. Russ, and A. Alcala. 2006. Gradients of abundance of fish across no-take marine reserve boundaries: evidence from Philippine coral reefs. Aquatic Conservation: Marine and Freshwater Ecosystems 16:349-371.

Abrahams, M. and M. Healy. 1990 Variation in the competitive abilities of fishermen and its influence on the spatial distribution of the British Columbia salmon troll fleet. Canadian Journal of Aquatic and Fisheries Sciences 47:1116-1121.

Attwood, C. 2003 Dynamics of the fishery for galjoen (*Dichistius capensis*) with an

assessment of monitoring methods. South African Journal of Marine Science 251:311-330.

Babcock, E. and A. MacCall. 2011. How useful is the ratio of fish density outside versus inside no-take marine reserves as a metric for fishery management control rules? Canadian Journal of Fisheries and Aquatic Sciences 68:343-359.

Beverton, R. and S. Holt. 1957. On the dynamics of exploited fish populations. [1993 reprint of the 1957 edition]. Chapman and Hall, London. 533 pp.

Bohnsack, J. 1999. Incorporating no-take marine reserves into precautionary management and stock assessment. NOAA Tech. Memo. NMFS-F/SPO-40. pp. 8-16.

Botsford, L., D. Brumbaugh, C. Grimes, J. Kellner, J. Largier, M. 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(1): 69-95.

CDFG. 2008. Channel Islands Marine Protected Areas: First 5 Years of Monitoring: 2003-2008. California Department of Fish and Game: (www.dfg.ca.gov/marine)

Caputi, N., R. Melville-Smith, S. de Lestang, J. How, A. Thomson, P. Stephenson, I. Wright, K. and Donohue. 2008. Draft Stock Assessment for the West Coast Rock Lobster Fishery. Western Australia Fisheries and Marine Research Laboratories, North Beach, Western Australia, Australia.

Chapman, M., and D. Kramer. 1999. Gradients in coral reef fish density and size across the Barbados Marine Reserve boundary: effects of reserve protection and habitat characteristics. Marine Ecology Progress Series 181:81-96.

Côté, I., I. Mosqueira, and J. Reynolds. 2001. Effects of marine reserve characteristics on the protection of fish populations: a meta analysis. Journal of Fish Biology 59 Supplement A:178-189.

DeMartini, E. 1993. Modeling the potential of fishery reserves for managing Pacific coral reef fishes. Fishery Bulletin 91:414-427.

Engle, J. 1979 Ecology and Growth of Juvenile California Spiny Lobster, *Panulirus interruptus* (Randall). Ph.D. dissertation, University of California Santa Barbara, California, USA: 298 pp.

García-Charton, J., and A. Pérez-Ruzafa. 1999. Ecological heterogeneity and the evaluation of the effects of marine reserves. Fisheries Research 42:1-20.

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 308:207-219.

Groenveld, J. 2000. Stock assessment, ecology and economics as criteria for choosing between trap and trawl fisheries for spiny lobster *Palinurus delagoae*. Fisheries Research 48:141-155.

Götz, A., S. Kerwath, C. Attwood, and W. Sauer. 2008. Effects of fishing on population structure and life history of roman *Chrysoblephus laticeps* (Sparidae). Marine Ecology Progress Series 362:245–259.

Guénette, S., T. Lauck, and C. Clark. 1998. Marine reserves: from Beverton and Holt to the present. Reviews in Fish Biology and Fisheries 8:251-272.

Haist, V., P. Breen, and P. Starr. 2009. A multi-stock, length-based assessment model for New Zealand rock lobster (*Jasus edwarsii*). New Zealand Journal of Marine and Freshwater Research 43:355-371.

Halpern, B. 2003. The impact of marine reserves: do reserves work and does reserve size matter? Ecological Applications 13 Supplement:S117-S137.

Harmelin-Vivien, M., L. Le Diréach, J. Bayle-Sempere, E. Charbonnel, J. García-Charton, D. Ody, A. Pérez-Ruzafa, O. Reñones, P. Sánchez-Jerez, and C. Valle. 2008. Gradients of abundance and biomass across reserve boundaries in six Mediterranean marine protected areas: Evidence of fish spillover? Biological Conservation 141:1829-1839.

Hartley, T., and R. Robertson. 2009. Stakeholder collaboration in fisheries research: integrating knowledge among fishing leaders and science partners in northern New England. Society & Natural Resources 22:42-55.

Hilborn, R., F. Micheli, and G. De Leo. 2006. Integrating marine protected areas with catch regulation. Canadian Journal of Fisheries and Aquatic Sciences 63:642-649.

Hilborn, R. and C. Walters. 1992. Quantitative Fisheries Stock Assessment: Choice, Dynamics and Uncertainty. New York, NY, USA: Chapman and Hall: 570 pp.

Kaunda-Arara, B., and G. Rose. 2004. Effects of marine reef National Parks on fishery CPUE in Coastal Kenya. Biological Conservation 118:1-13.

Kay, M., H. Lenihan, C. Guenther, J. Wilson, C. Miller, and S. Shrout. *In press*. Collaborative assessment of spiny lobster (*Panulirus interruptus*) population and fisheries responses to a marine reserve network. Ecological Applications.

Kay, M., H. Lenihan, C. Miller, and K. Barsky. 2008. Numbers, body size, and movement of lobster. In: Airame S, Ugoretz J (eds) Channel Islands Marine Protected Areas: First 5 Years of Monitoring. Cal Dep Fish Game, Santa Barbara, pp. 8-9.

Kellner, J., I. Tetreault, S. Gaines, and R. Nisbet. 2007. Fishing the line near marine reserves in single and multispecies fisheries. Ecological Applications 17:1039-1054.

Kelly, S., D. Scott, A. MacDiarmid, and R. Babcock. 2000. Spiny lobster, *Jasus edwarsii*, recovery in New Zealand marine reserves. Biological Conservation 92:359-369.

Lester, S., B. Halpern, K. Grorud-Colvert, J. Lubchenco, B. Ruttenberg, S. Gaines, S. Airame, and R. Warner. 2009. Biological effects within no-take marine reserves: a global synthesis. Marine Ecology Progress Series 384:33-46.

Macpherson, E., A. García-Rubies, and A. Gordoa. 2000. Direct estimation of natural mortality rates for littoral marine fishes using population data from a marine reserve. Marine Biology 137:1067-1076.

McGilliard, C., R. Hilborn, A. MacCall, A. Punt, and J. Field. 2010. Can information from marine protected areas be used to inform control-rule-based management of small scale, data-poor stocks? ICES Journal of Marine Science 68:201-211.

Moffitt, E., L. Botsford, D. Kaplan, and M. O'Farrell. 2009. Marine reserve networks for species that move within a home range. Ecological Applications19:1835-1847.

Polacheck, T. 1990. Year around closed areas as a mangement tool. Natural Resource Modeling 4:327-354.

Pollock, D. 1981. Population dynamics of rock lobster Jasus tristani at the Tristan da Cunha group of islands. Fisheries Bulletin of South Africa 15:49-66.

Quinn, T., and R. Deriso. 1999. Quantitative Fish Dynamics. Oxford University Press, New York, NY, USA: 560 pp.

Sánchez-Lizaso, J., R. Goñi, O. Reñones, J. García-Charton, R. Galzin, J. Bayle, P. Sánchez-Jerez, A. Pérez-Ruzafa, and A. Ramos. 2000. Density dependence in marine protected populations: a review. Environmental Conservation 27:144-158.

Shears, N., R. Grace, N. Usmar, V. Kerr, and R. Babcock. 2006. Long-term trends in lobster populations in a partially protected vs. no-take marine park. Biological Conservation 132:222-231.

Sparre, P., and S. Venema. 1998. Introduction to Tropical Fish Stock Assessment. FAO Fisheries Technical Paper 306/1 Rev. 2. FAO, Rome.

Swain, D., and E. Wade. 2003. Spatial distribution of catch and effort in a fishery for snow crab (*Chionoecetes opilio*): tests of predictions of the ideal free distribution. Canadian Journal of Aquatic and Fisheries Sciences 60(8): 897-909.

Taylor, B., and J. McIlwain. 2010. Beyond abundance and biomass, effects of marine protected areas on the demography of a highly exploited reef fish. Marine Ecology Progress Series 411:243-258.

Walters, C., 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 64:1009-1018.

Willis, T., and R. Millar. 2005. Using marine reserves to estimate fishing mortality. Ecology Letters 8:47-52.

Willis, T., R. Millar, R. Babcock, and N. Tolimieri. 2003. Burdens of evidence and the benefits of marine reserves: putting Descartes before des horse? Environmental Conservation 30:97-103.

Wilson, J., J. Prince, and H. Lenihan. 2010. A management strategy for sedentary nearshore species that uses marine protected areas as a reference. Marine and Coastal Fisheries: Dynamics, Management and Ecosystem Science 2:14-27.

Wilson, J. 2011. Marine reserves and the management of small scale fisheries. Ph.D. dissertation. University of California Santa Barbara, California, USA: 155pp.

Table 3.1. Linear regression tests of the effects of location inside versus outside reserves and distance from reserve borders (predictor variables) on mortality (response variable) across sampling sites. Values reported for predictor variables include the coefficient (β), the t-statistic, and the *P* value.

	In vs. Out (Eq. [6])			Distance In / Out (Eq. [7])		
	β	***t***	***P***	β	***t***	***P***
In_reserve	**-0.37**	**-6.15**	**<0.001**	--	--	--
Distance_in	--	--	--	**-1.1e^{-4}**	**-3.75**	**0.003**
Distance_out	--	--	--	4.7e^{-5}	2.06	0.063
Gull		omitted		-0.11	-1.110	0.295
Scorpion	0.06	1.12	0.286		omitted	
Carrington	4.5e^{-3}	0.06	0.957	-0.04	-0.55	0.593
Constant	**0.57**	**9.87**	**<0.001**	**0.47**	**7.43**	**<0.001**
Observations		16			9 (in) / 7 (out)	
r^2		0.78			0.70	

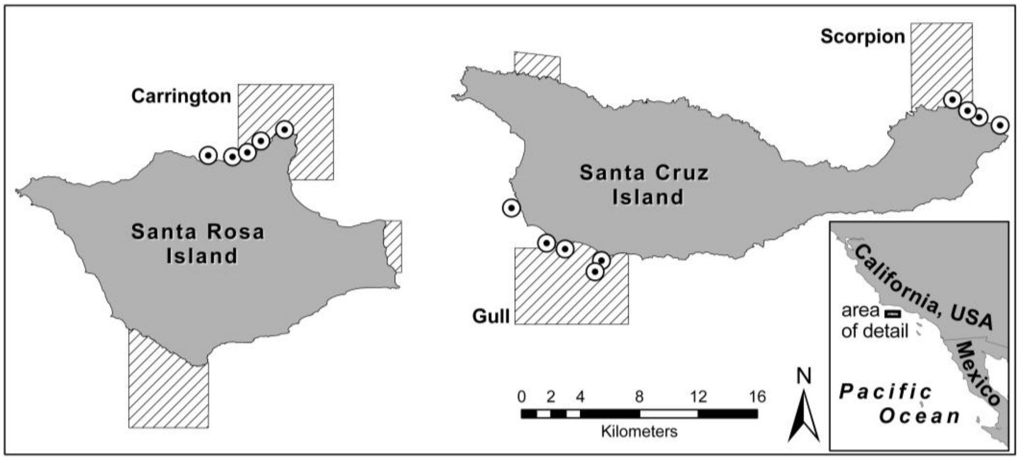

Figure 3.1. Map showing marine reserves (hashed areas) at Santa Cruz Island and Santa Rosa Island, part of the northern Santa Barbara Channel Islands, in the Southern California Bight (inset). Sampling sites at the Carrington, Gull, and Scorpion reserves are indicated as points within and near each reserve.

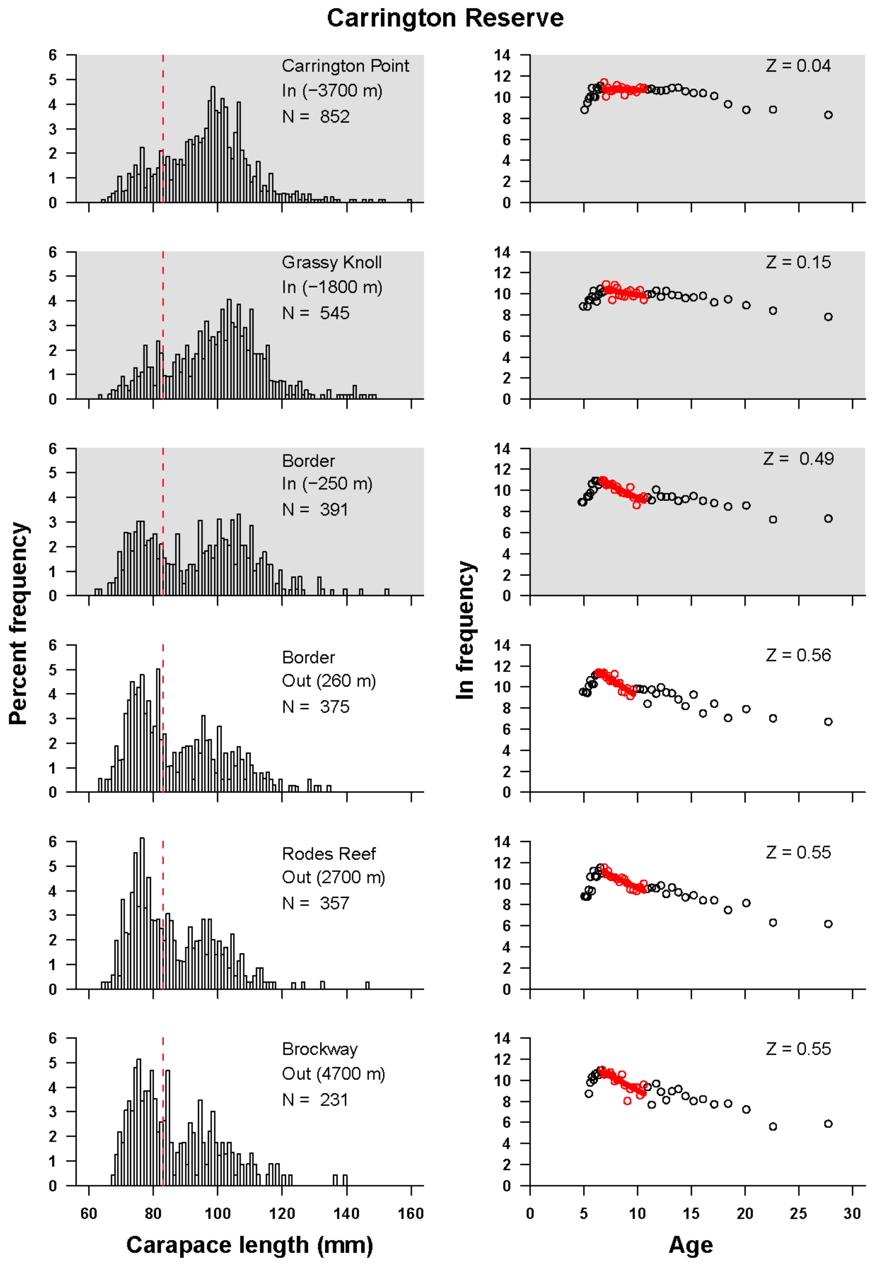

Figure 3.2. Length frequency distributions (left column of panels) and linearized catch curve (LCC) plots (right column of panels) for female lobsters sampled at sites in or near the Carrington marine reserve. Length frequencies and LCC plots for a single site are adjacent panels. Sites inside reserves are shaded gray. Also reported in length frequency panels are the distances of sampling sites from the nearest reserve border (negative values for sites inside reserves) and the number of lobsters in each sample. Dashed line represents the minimum legal size limit (82.5 mm). Total mortality (*Z*) at each site is reported on the LCC panels.

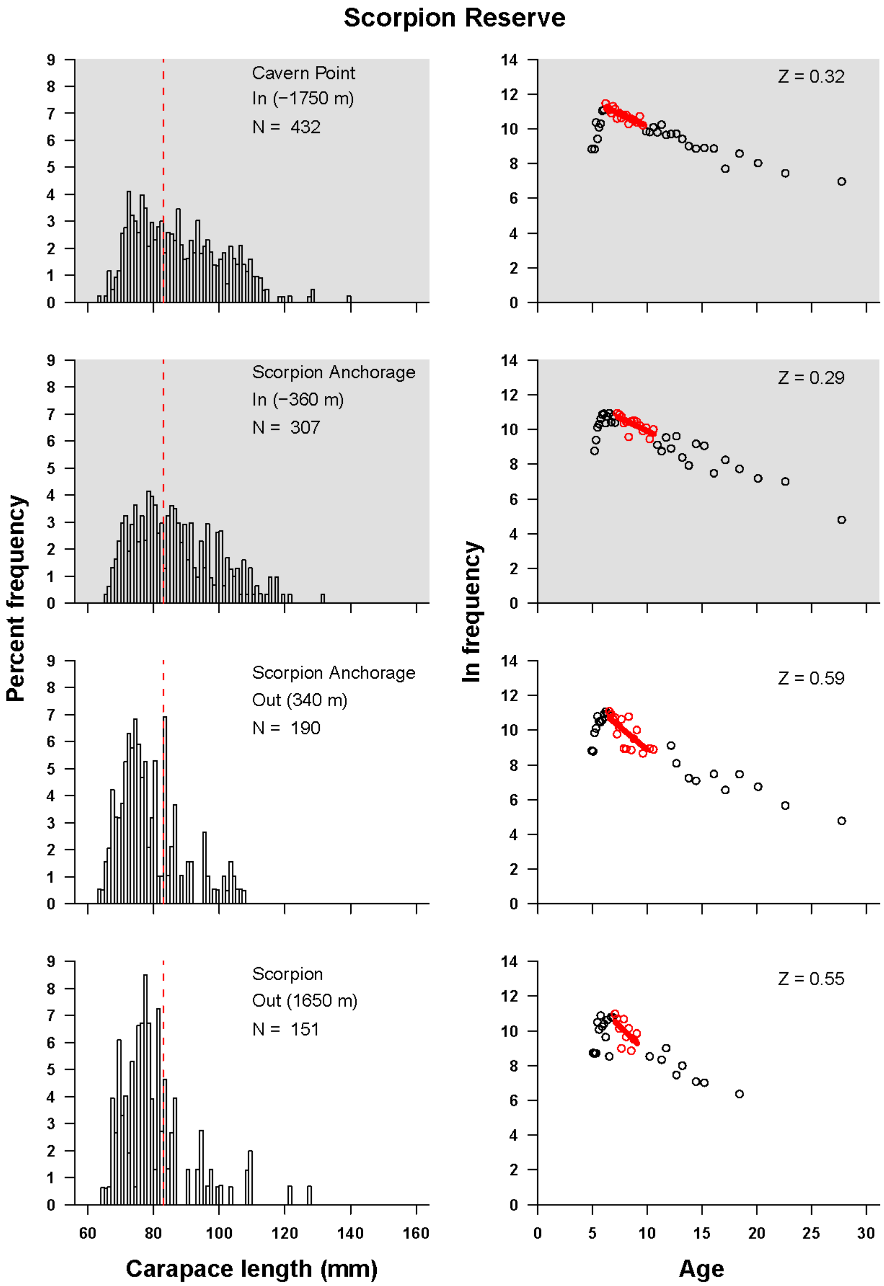

Figure 3.3. Length frequency distributions (left column of panels) and linearized catch curve (LCC) plots (right column of panels) for female lobsters sampled at sites in or near the Scorpion marine reserve. All other details in Figure 3.3 are analogous to details described for Figure 3.2.

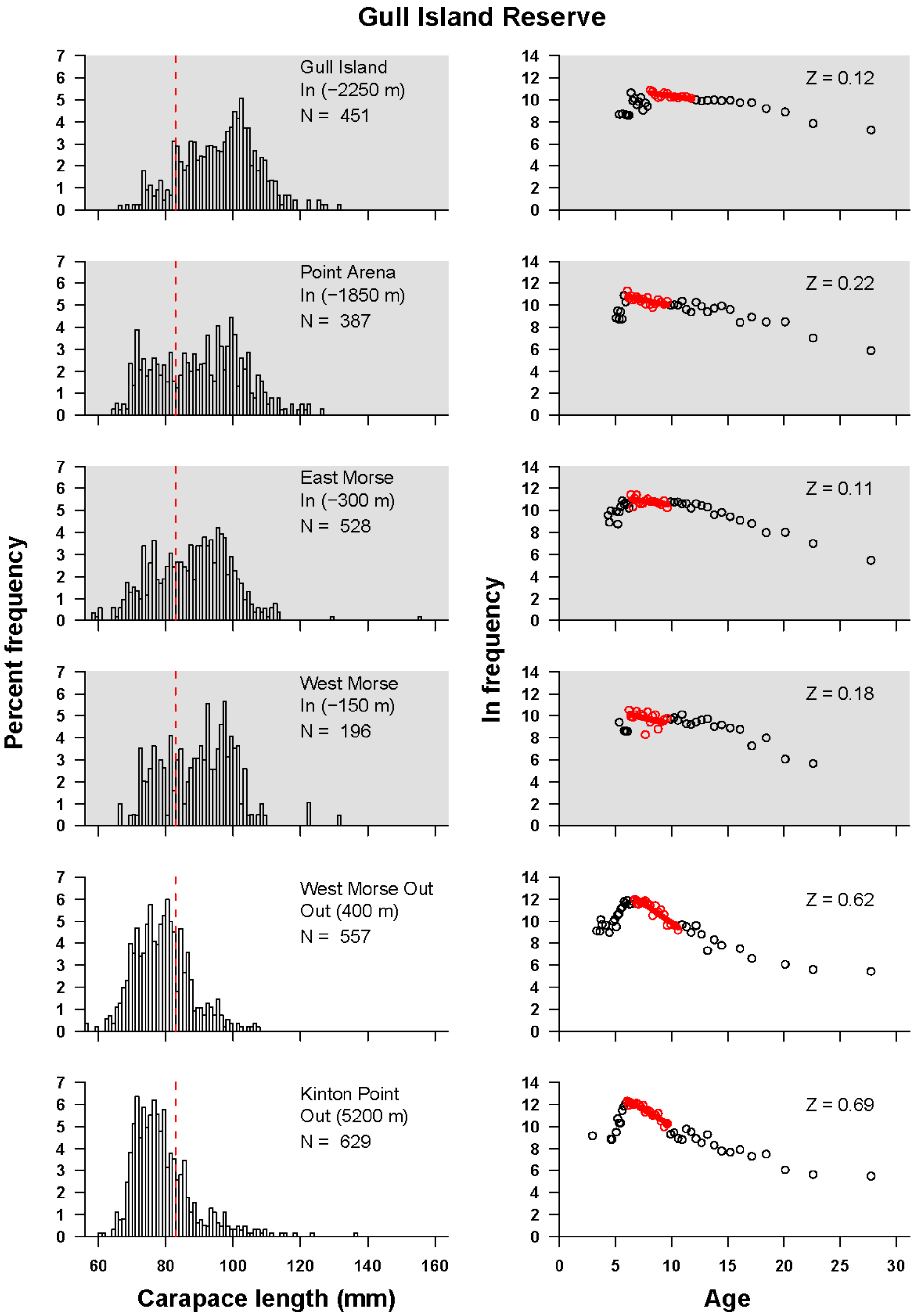

Figure 3.4. Length frequency distributions (left column of panels) and linearized catch curve (LCC) plots (right column of panels) for female lobsters sampled at sites in or near the Gull marine reserve. All other details in Figure 3.4 are analogous to details described for Figure 3.2.

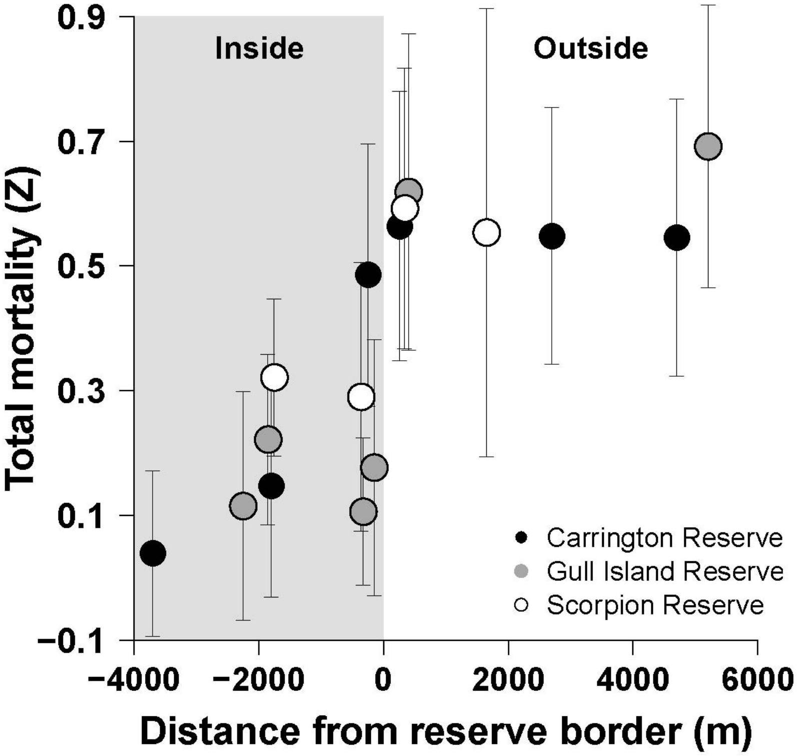

Figure 3.5. Mean total mortality (*Z*), estimated with LCC, and the distance from nearest marine reserve border for of each of the 16 sites associated with the Carrington, Gull, and Scorpion reserves. Gray shading indicates sites inside reserves. Error bars are 95% confidence intervals. Mean values for each site shown in this figure were used in subsequent regression analyses.

CHAPTER 4

A Collaborative, Reserve-Based, and Spatially Explicit Harvest Rate Assessment For the Small Scale Fishery for California Spiny Lobster

INTRODUCTION

Industrialization of fisheries in the 20th century has facilitated unprecedentedly large scale harvests in the world's oceans (Iudicello et al. 1999, Lotze et al. 2006), but small scale fisheries remain equally important for global employment and food supply. For example, more than 90% of all the world's fishermen work in small scale fisheries, which in turn employ an additional 100 million people working in support industries (Béné et al. 2007), and these fisheries account for more than half of the world's annual fish catch (Berkes et al. 2001). Because small scale fisheries focus on small stocks, and often occur in developing countries, resources for management and assessment are often inadequate. Therefore, against a backdrop of full exploitation and/or decline in those fisheries for which assessments exist (Hilborn et al. 2003, Mullon et al. 2005, Branch et al. 2011), the story of individual small scale fisheries plays out in the absence of formal assessments and with high degrees of management uncertainty.

There are two primary challenges for assessment of small scale fisheries: cost effectiveness and spatial relevance. Traditional stock assessments require data and analytical expertise that can be expensive relative to the economic value of an individual fishery, and therefore may not be deemed important by the political jurisdictions in which fisheries operate. Small scale fisheries in California exemplify this reality. Total revenue from California's commercial fisheries in 2007 was $120.2 million (Harty et al. 2010), which is less than that 0.007% of the state's GDP. By comparison, California farming income in 2007 was $39 billion (or ~325x the economic value of fishing). These economic realities suggest that broad increases in governmental spending for fisheries assessments are unlikely, and it is therefore naïve and unfair to expect improved assessment capability from underfunded resource managers. The second challenge is that population dynamics for marine species are geographically variable due to environmental conditions that change across space (e.g., MacCall 1990). Evidence suggest that this variability is high among demersal nearshore species (Campbell and Robinson 1983, Morgan et al. 2000, Prince 2005). Additionally, fleet dynamics can be variable across space (Prince and Hilborn 1998). Consequently, small scale nearshore fisheries are spatially structured and may best be assessed and managed with techniques that account for this (Orensanz and Jamieson 1998).

Recently, two specific remedies for assessment challenges stemming from costs and spatial structure have begun to emerge. The first is the use of populations inside reserves as references for unfished populations (Babcock and MacCall 2010, McGilliard *et al*. 2010, Wilson *et al*. 2010) or for estimating life history parameters used in fishery assessments (Bohnsack 1999, MacPherson *et al*. 2000; Taylor and McIlwain 2010). Such assessments can be relatively low cost, are applicable in data poor conditions, and are spatially explicit on scales that are relevant to local biological conditions and fishing fleet dynamics. Another important tool is collaborative fisheries research (CFR) in which commercial fishermen and fisheries scientists work together to improve the quality and quantity of information available for management (NRC 2004).

In this chapter I build upon results of chapter 3 to provide a harvest rate assessment for the small scale nearshore fishery for California spiny lobster (*Panulirus interruptus*) at the Santa Barbara Channel Islands, California USA. This assessment strategy is spatially explicit and reserve-based, and mobilizes commercial fishermen and fisheries scientists in a novel collaboration in which reserve monitoring was structured to provide data necessary for the assessment. The assessment provided in this chapter was accomplished with two steps: (1) estimation of harvest rates from the total mortality estimates inside and outside reserves as reported in Chapter 3, and; (2) interpretion of the harvest rates in the context of yield per recruit (YPR) and spawning potential ratio (SPR) models that I constructed for *P. interruptus*. This work provides a practical, cost effective, and community based method for assessment of small scale fisheries, which is crucial because such fisheries are globally important but are under assessed, and it is a pioneering example for enhanced management though the integration of collaborative fisheries research and the use marine reserves as fisheries assessment tools.

MATERIALS AND METHODS

Harvest rate estimates

I estimated fishing mortality (F) from data reported in Chapter 3 by subtracting mortality rates inside reserves from the total mortality (Z) measured on the fishing grounds. The rationale is that total mortality on fishing grounds (Z_{fished}) is comprised of natural mortality (M) and mortality due to fishing (i.e., $Z_{fished} = M + F$). Therefore, calculation of F requires knowledge of M, which I estimated from sampling inside reserves where fishing is prohibited (i.e., inside reserves, $Z_{reserve} = M$). The natural mortality rate I use from inside reserves was the average reported in Chapter 3 from sites near reserve interiors (i.e., $M = 0.169$), but excludes estimates from sites near reserve borders (mean M including those sites = 0.212). This was motivated by results of Chapters 2 and 3, which indicate that spillover is likely at the Santa Barbara Channel Island (SBCI) reserves, such that mortality rates immediately inside reserve borders are probably influenced by fishing and likely overestimate M. The values for Z and M that are generated by the linearized catch curve (LCC) analysis reported in Chapter 3 are instantaneous rates, and in this chapter I converted natural mortality rates (M) for each site to annualized natural mortality rates (m; the proportion of a population that dies annually due to non-human causes). These estimates for m were then subtracted from annualized total mortality estimates in order to calculate an annualized harvest rate at each site. This was accomplished with the following equations:

$$a_i = 1 - e^{-Z_i} \quad (1)$$

where a_i is the annualized total mortality (i.e., the proportion of the population that dies annually due to fishing and natural mortality) at each site i, Z_i is the instantaneous total mortality at each site i, and values for Z_i are from the LCC analysis in Chapter 3. It then follows that:

$$m_i = a_i\left(\frac{\overline{M}}{Z_i}\right) \quad (2)$$

where m_i is the annualized natural mortality rate at each site i, and $\overline{M}$ is the mean instantaneous natural mortality from the five sites near reserve interiors (calculated from results of Chapter 3). Harvest rate is calculated subsequently:

$$u_{i,f} = a_i\left(\frac{F_{i,f}}{Z_{i,f}}\right) \quad (3)$$

where $u_{i,f}$ is the annualized harvest rate (i.e., the proportion of the population that is removed annually via fishing) at each site i outside reserves where fishing (f) takes place, and $F_{i,f}$ is the instantaneous fishing mortality at individual site i as calculated from the equation $Z_{i,f} = \overline{M} + F_{i,f}$. (values for $Z_{i,f}$ and $\overline{M}$ are from

Chapter 3). Conversions to annualized rates were made to ease interpretation of results because annualized rates are more intuitive to understand. In addition to converting from instantaneous to annualized rates, equations (2) and (3) provide an important adjustment to natural mortality rates based on site specific total mortality. Failure to do so results in overestimates of natural mortality at each site because fishing decreases the effective rate at which animals die of natural causes (because they are caught before dying of natural causes) such that effective *m* in fished areas is actually lower than estimates in the absence of fishing (i.e., inside reserves). Failure to adjust for this decreases rate of natural mortality leads to underestimates of harvest rates.

Yield per recruit (YPR) and spawning potential ratio (SPR) models

To provide a frame of reference for the harvest rates I estimated, I constructed yield per recruit (YPR) and spawning potential ratio (SPR) models for *P. interruptus*. The YPR and SPR models were based upon an age structured model in which recruitment (the # of 0-1 year old lobsters) was constant and the length of lobsters in each age class was determined by parameters of the von Bertalannfy growth function (VBGF; equation 4):

$$L_t = L_\infty \left(1 - \exp\left(-K\left(t - t_0\right)\right)\right) \qquad (4)$$

where L_t is the length of individuals at age t, L_∞ is the mean asymptotic length, K is the growth rate, and t_0 is the theoretical length at age zero. I estimated these parameters from lobsters that were tagged and recaptured over a three year period from 2006-2009 at my field sites inside reserves (Fig. 1, Chapter 3). VBGF parameters were estimated using an expression of the VBGF that is explicitly designed for use with tag-recapture data where length at initial tagging, the length at recapture, and time elapsed between tagging and recapture are used to estimate K and L_∞ (Quinn and Deriso 1999). This expression takes the following form (equation 5):

$$\Delta L_j = (L_\infty - L_{ij})(1 - e^{-K\Delta tj}) \qquad (5)$$

where ΔL_j is the change in length (growth increment) between tagging and recapture for individual lobster j, L_{ij} is the intial length of lobster j at tagging, Δtj is the time elapsed between initial tagging and recapture for individual j, and K and L_∞ are free parameters estimated by the model.

Several aspects of the recapture data used to estimate K and L_∞ warrant mention: (1) t_0 is not estimable from tag-recapture data alone and by convention we assume $t_0 =$ zero; (2) reliable estimates for K and L_∞ were not obtained for male lobsters because growth increments for male lobsters showed no clear trend of decreasing across the length classes that were tagged in this study, and as a consequence L_∞ was not estimable. Therefore, the present analysis considers female lobsters only; (3) I fit equation 3 to lobsters that were captured within 3 weeks of the anniversary of initial tagging in order to minimize bias that results from seasonal and incremental growth over very short time intervals or during time periods that do not include all annual seasons; (4) I use data only from lobsters that were tagged and recaptured inside reserves in order to avoid underestimates of K due to differential harvest of fast growing individuals, and underestimates for L_∞ due to truncated size structure of fished populations. With regard to the final point, lobster populations inside reserves are not likely to be at virgin (i.e., pre-fishing) conditions and so L_∞ may be an underestimate. Future monitoring of reserves is necessary to resolve this issue.

Once the age-length relationship was established using VBGF parameter estimates from my tag-recapture data, I specified a YPR model that illustrates how theoretical yield to the fishery changes across a range of harvest rates. This YPR model took the following form (equation 6):

$$YPR = \sum_{i=1}^{n} W_i V_i S_{ih} \qquad (6)$$

where n is the number of age (year) classes in the population; W_i is the mean weight of individuals in age class i; V_i is the vulnerability to fishing gear of individuals in age class i; $S_{ih} = (1- m_{ih}) * (1-u_{ih}V_{ih})$, the annual survival of individual lobsters to age class i from age class h (i.e., h = year class i-1); u_{ih}= the annual harvest rate of females of age i when they were in year class h; m_{ih} = the annual natural mortality rate of females of age *i* when they were in year class *h*; and V_{ih} is the vulnerability to fishing gear of lobsters in age class *i* when they were in age class *h*.

Spawning potential ratio (SPR) is the ratio of egg production of a single recruit under a given fishing mortality rate relative to that of an unfished recruit throughout its lifetime. The first step in calculating SPR is to estimate spawning stock biomass per recruit (SSBR; equation 7):

$$SSBR = \sum_{i=1}^{n} f_i p_i S_{ih} \qquad (7)$$

where *n* = number of ages in an unfished population; f_i is the mean fecundity of females at age *i*; p_i is the proportion of females in age class *i* that are sexually mature (size at maturity, or SAM), and S_{ij} is as described above for YPR. SPR is then calculated with equation 8:

$$SPR = \frac{SSBR_{fished}}{SSBR_{unfished}} \qquad (8)$$

Equations 6-8 describing YPR and SPR were applied over all possible harvest rates (i.e., all *u* between 0-1), and in an additional analysis that interacts all harvest rates across a range of sizes at which female lobsters are first captured in the fishery. The result is two theoretical relationships: (1) a two dimensional relationship between YPR / SPR and all harvest rates, and; (2) a three dimensional relationship between YPR / SPR (z-axes values), harvest rates (x-axis), and size at first capture (y-axis). In models 6-8, the length-weight relationship (i.e., W_i for all i's) was estimated from data collected by working with a commercial fisherman (Chris Miller) to measure and weigh all lobsters caught from Santa Cruz Island on two dates during the 2008-2009 season. Similarly, V_i was estimated from size classes of lobsters captured during my research trapping in a subset of traps that had standard commercial escape ports installed, and p_i and f_i were estimated from data reported for *P. interruptus* in California by Allen (1916), Fry (1928, in Wilson 1948), and Lindberg (1955). Equations were fit to each of the datasets describing growth (VBGF), W_i, V_i, f_i, and p_i using maximum likelihood to determine the best fit to each. Equations and parameter values describing these best fits for are reported in the results section (VBGF equation described above). Uncertainty around YPR and SPR was characterized by bootstrapping VBGF parameter estimates as described in Chapter 3.

RESULTS

Harvest rate estimates

The mean estimate of instantaneous natural mortality ($\overline{M}$) from my five sites near reserve interiors was 0.169 (± 0.048 SE). Instantaneous total mortality rates (Z) ranged from 0.039- 0.692, which translated to annualized mortality rates (a) that ranged from 0.038 - 0.49 (Table 1). Estimated natural mortality rates ranged between 0.134-0.166 (inside reserves) and 0.122-0.130 (outside reserves). Annualized harvest rates outside reserves ranged from 0.290 – 0.377. Mean harvest rates for sites associated with each reserve were 0.294 (Carrington), 0.307 (Scorpion), and 0.355 (Gull). The grand mean of these three means was 0.319 (± 0.019 SE), and this value is reported in the context of the YPR and SPR models I specified for *P. interruptus*.

Yield per recruit (YPR) and Spawning potential ratio (SPR) models

The annualized natural mortality rate that I used in my models ($m = 0.159$), was the mean of m values from the five sites at reserve interiors (Table 1). Growth increments for female lobsters were highest among the smaller lobsters I tagged in this study, and they steadily decreased with increased initial carapace length (Figs. 1 and 2). In contrast, growth increments for male lobsters were highest at intermediate initial sizes (e.g., ~90 - 120 mm) and they do not show a strong trend of decreasing towards zero among the largest size classes I was able to tag and recapture. The latter trend made fitting the VBGF to these data impractical without a "best-guess" *a priori* selection of L_∞ from historical data – a practice that I decided against. Bootstrapped best fits to female growth increment data, including measurements from Jack Engel's 1979 dissertation (Fig 2), estimate L_∞ at 121.077 mm (± 4.60 SD) with a K of 0.105 (± 0.01 SD). These data from Engel were included because I was unable to capture small juveniles using the traps I deployed.

Best fits to weight at length data measured by port sampling commercial catch indicate exponential relationships for both males and females (Fig. 3). Females are heavier than males at a given carapace length because the ratio of tail size to carapace length is greater in females than in males. This is due partially to the fact that females brood their eggs on the underside of their tails, and larger tails may be necessary for increased fecundity. The best fit to fecundity at size data from Allen (1916) and Lindberg (1955) was linear and steep (Fig. 4). An exponential fit was also examined but had a significantly higher AIC value than the linear fit reported here. Size at sexual maturity (SAM), also defined as the proportion of females in each size class that were sexually mature, and which was estimated from data reported by Fry (1928; in Wilson 1948) and Lindberg (1955), was best described by a logistic function (Fig. 5). Finally, selectivity of commercial traps was knife edged and centered on the legal size (82.5 mm) for *P. interruptus*. Consequently, vulnerability in my YPR and SPR models was set at zero for all age classes in which lobsters were < 82.5 mm, and set at one (i.e., animals were fully vulnerable to gear) for age classes in which lobsters were > 82.5 mm.

The YPR model that I specified using $m = 0.159$ and the relationships I described for growth (length at age), weight at length, fecundity, SAM, and vulnerability at the current legal size limit (82.5 mm) indicates a range of *pretty good yield* (PGY; see *Discussion* section of this chapter) that begins at ~0.2 (Fig. 7A and 8A). The SPR model indicates rapid loss of spawning potential even at low-moderate harvest rates (Fig. 7B), and the relationship holds at all minimum sizes lower than ~90 mm (Fig. 8B).

DISCUSSION

The grand mean of the harvest rates I estimated for my sites at Santa Cruz and Santa Rosa Islands is within the range of pretty good yield (PGY) defined by Hilborn (2010) as any yield that achieves 80% of a theoretical maximum. The concept of PGY was born out of the recognition that maximum sustainable yields are inherently unattainable due to stochastic human and environmental factors that drive fisheries productivity. The annual harvest rate of 0.319 is interpreted to mean that 31.9% of all legal lobsters are harvested every year. The harvest rate estimated here is low relative to other spiny lobster fisheries across the globe (Kagwade 1993, Lipcius et al. 2001, Mateo and Tobias 2002, Caputi et al. 2008), and is much lower than the verbal declarations of u = 0.7-1.0 issued by some California marine scientists, resource managers, and environmental NGO's.

Although harvest rates of *P. interruptus* at my SBCI sites are suggestive of a generally healthy and sustainable fishery, the results should be interpreted with caution. There are several reasons this is true. First, the fishery at SBCI is probably not at equilibrium because effort (number of traps) continues to increase. This increased effort is driven in part by ex-vessel prices that recently increased to ~\$18 lb^{-1} (from ~\$9 lb^{-1} only 5-6 years ago). Secondly, harvest rates are near asymptotic yield values (Figs. 7A and 8A) such that increased effort will likely not result in proportional increases in yield but will reduce the spawning potential for this stock (Figs. 7B and 8B). Finally, the LCC and YPR model used to estimate and assess the harvest rates are equilibrium models that assume stability in parameters that are likely to be temporally variable. For example, the L_∞ value used is likely to increase in the future because lobster populations inside reserves probably remain truncated to some extent due to fishing prior to reserve establishment (in April 2003). Thus, continued growth resulting in increased mean size of lobsters inside reserves will lead to larger estimates of L_∞. The effect of increased L_∞ (and corresponding K values) on both the harvest rate estimates and YPR models should be considered. Additionally, the YPR model assumes constant recruitment, although recruitment dynamics for *P. interruptus* in California are not well understood. It is possible that any shift in oceanographic conditions (e.g., PDO regime) that reduces recruitment will adversely affect YPR. Finally, harvest rates that optimize fishery yield may still have deleterious or unwanted ecological consequences.

The uniformly negative potential consequences of increased harvest rates at SBCI suggest that effort control may be a valuable goal for this fishery. Indeed, in the early 1990’s the California Lobster and Trap Fishermen’s Association (CLTFA) and the California Department of Fish and Game (CDFG) mutually identified the need to limit the number of participants in the commercial fishery (K. Barsky, CDFG, *personal communication*). The result was a 1994 moratorium on new permits and a restricted access program that was implemented in 1996

(Barsky et al. 2004). Permits became transferrable in 2005 for fishermen meeting landings requirements (those not meeting requirements retained a non-transferrable permit valid for the lifetime of the permit holder). The current limited entry system does not include a mechanism to reduce effort or harvest rates, and as such it is fair to say that it does more to ensure economic stability for lobster fishermen than it does to reduce capacity. CLTFA and CDFG managers intended for transferability to be accompanied by a trap limit, but the proposal was deemed impossible to enforce by CDFG wardens. As a consequence, transferability was implemented without a trap limit. Interest in a trap limit remains high among many commercial fishermen who are concerned about latent capacity, especially as rising ex-vessel prices (from ~ $9/lb in 2005-06 to ~ $18/lb in 2010-11), displacement due to marine reserves, and transfer of latent permits to active fishermen all lead to increased effort. Capacity adjustments to the commercial sector may stimulate similar actions for the recreational sector, and allocation within and between sectors promises to be a contentious and difficult consideration for managers.

Harvest rates assessed here for the northern SBCI are likely to be lower than rates at most other fishing grounds in California. This is true because size structure at SBCI is larger than at reefs along the mainland coast and some Southern Channel Islands, where length frequencies are truncated and indicate much higher harvest rates. These higher exploitation rates, when considered in the context of the SPR model constructed here, indicate that effort reduction along the mainland has especially strong potential to improve spawning potential. The time required to realize SPR increases is possibly short-term, given the rapid population increases described in Chapter 1 of this dissertation. Finally, any SPR increases realized through effort reduction would be complemented by economic benefits due to cost elimination. Therefore, the potential for effort reduction to increase biological yield (assuming a stock-recruitment relationship exists) and cut costs to fishermen presents a two-pronged mechanism by which the fishery for *P. interruptus* may become more profitable for the fishermen and fishing communities of southern California.

The SPR model reported here indicates that reproductive output deceases drastically under any harvest schemes that achieve PGY. The mean harvest rate of 0.319 (± 0.019 SE) translates to an SPR of ~0.23 (bounded with 95% confidence intervals at 0.19 and 0.31). This indicates that current reproductive output at SBCI is ~23% of virgin (i.e., pre-fishing) conditions. The implications of this SPR for fishery sustainability are not clear for two reasons. First, crustacean fisheries are known for their stability even at extremely low egg production. For example, egg production in of *Homarus americanus* off the east coast of North America is thought to be well below 10% of virgin conditions, and in Canadian waters has been estimated to be at ~1-2% of prefishing levels (Ennis and Fogarty 1997). Secondly, sock-recruitment dynamics are not well understood for *P. interruptus*, especially for southern California where recruitment may be highly episodic and potentially influenced by larval input form Mexico (Pringle 1986).

An important consideration in estimating harvest rates when reserves are present is that a significant fraction of the stock (in reserves) is not vulnerable to harvest. The inclusion of this portion of the stock in assessments is gaining attention and is a challenge for stock assessment science (Bohnsack 1999, Field 2006). A simplistic approach that can be used with the results presented here is multiply the harvest rate by the portion of the fishing ground that is open to harvest. For example, it is estimated at that ~30% of the rocky bottom (i.e., lobsters habitat) at SBCI is inside reserves. Therefore, an adjusted harvest rate that "credits" the fishery for the potion of the stock inside reserves is 0.22 (0.319 x 0.7 = 0.22). Due to this effect reserves may provide a buffer for reference points such as SPR (Bohnsack 1999). This adjusted harvest rate indicates how reserves might have caused increased harvest rates outside existing reserves (compared to pre-reserve conditions in which effort was distributed across reserve areas prior to their closure [Fig. 7A and 8A]) , and its affect on SPR (Figs. 7B and 8B).

The assessment strategy presented here can be readily applied across the entire range of *P. interruptus*. Although life history characteristics (e.g., L_∞, K) for this species are likely to vary throughout southern California, the marine reserve network designed for this region (established October 2011) likely encompasses the physical and biological variability that in turn drives life history variability. Therefore, the collaborative and spatially explicit approach developed here may be appropriate for distribution throughout California. The CLTFA and DFG are interested in geographically expanding collaborative work such as this, at least partially as a means to provide marine reserve monitoring, and consequently joint proposals have been prepared to seed expansion of this program. It may come to pass that the work reported here marks an initial stage of broader collaborative and spatially explicit assessment and management of *P. interruptus* throughout California.

LITERATURE CITED

Allen, B. 1916. Notes on the spiny lobster (*Panulirus interruptus*) of the California coast. University of California Publications in Zoology 16:139-152.

Babcock, E., and A. MacCall. 2011. How useful is the ratio of fish density outside versus inside no-take marine reserves as a metric for fishery management control rules? Canadian Journal of Fisheries and Aquatic Science 68: 343-359.

Béné, C., G. MacFadyen, and E. Allison. 2007. Increasing the contribution of small-scale fisheries to poverty alleviation. FAO Fisheries Technical Paper 481. FAO, Rome.

Berkes, F., R. Mahon, P. McConney, R. Pollnac, and R. Pomeroy. 2001. Managing small-scale fisheries: alternative directions and methods. International Development Research Centre, Ottawa. 309 pp.

Bohnsack, J. 1999. Incorporating no-take marine reserves into precautionary management and stock assessment. NOAA Tech. Memo. NMFS-F/SPO-40. pp. 8-16.

Branch, T., O. Jensen, D. Ricard, Y. Ye, and R. Hilborn. 2011. Contrasting global trends in marine fishery status obtained from catches and from stock assessments. Conservation Biology – early view online: http://onlinelibrary.wiley.com/doi/10.1111/j.1523-1739.2011.01687.x/abstract

Campbell, A., and D. Robinson. 1983. Reproductive potential of three American lobster (*Homarus americanus*) stocks in the Canadian Maritimes. Canadian Journal of Fisheries and Aquatic Sciences 40:1958-1967.

Caputi, N., R. Melville-Smith, S. de Lestang, J. How, A. Thomson, P. Stephenson, I. Wright, and K. Donohue. 2008. Draft Stock Assessment for the West Coast Rock Lobster Fishery.

Ennis, G., and M. Fogarty. 1997. Recruitment overfishing reference point for the American lobster, *Homarus americanus*. Marine and Freshwater Research 48:1029-1034.

Field, J., A. Punt, R. Methot, and C. Thomson. 2006. Does MPA mean 'Major Problem for Assessments'? Considering the consequences of place-based management systems. Fish and Fisheries 7:284-302.

Fry, D.H. Jr. 1928. Unpublished manuscript of work on spiny lobsters at La Jolla.

Harty, J.M., Healey, M.C., Iudicello, S., Dewitt, J, Kirlin, J.J., and R. Larson. 2010. Lessons learned from California's Marine Life Management Act. California Ocean Protection Council.

Hilborn, R. 2010. Pretty Good Yield and exploited fisheries. Marine Policy 34:193-196.

Hilborn, R., T. Branch, B. Ernst, A. Magnusson, C. Minte-Vera, M. Scheuerell, and J. Valero. 2003. State of the world's fisheries. Annual Review of Environment and Resources 28:359-399.

Iudicello, S., Weber, M., and R. Wieland. 1999. Fish, Markets, and Fishermen: The Economics of Overfishing. Island Press, Washington D.C.

Kagwade, P. 1993. Stock assessment of the spiny lobster *Panulirus polyphagus* (Herbst) off north-west coast of India. Indian Journal of Fisheries 40:63-73.

Lindberg, R.G. 1955. Growth, population dynamics, and field behavior in the spiny lobster, *Panulirus interruptus* (Randall). University of California Publications in Zoology 59:157-248.

Lipcius, R., W. Stockhausen, and D. Eggleston. 2001. Marine reserves for Caribbean spiny lobster: empirical evaluation and theoretical metapopulation recuitment dynamics. Marine and Freshwater Research 52:1589-1598.

Lotze, H., H. Lenihan, B. Bourque, R. Bradbury, R. Cooke, M. Kay, S. Kidwell, M. Kirby, C. Peterson, and J. Jackson. 2006. Depletion, degradation, and recovery potential of estuaries and coastal seas. Science 312:1806-1809.

Macpherson, E., A. García-Rubies, and A. Gordoa. 2000. Direct estimation of natural mortality rates for littoral marine fishes using population data from a marine reserve. Marine Biology 137:1067-1076.

MacCall, A. 1990. Dynamic Geography of Marine Fish Populations. Washington Sea Grant, Seattle.

Mateo, I., and W.J. Tobias. 2002. Preliminary estimates of growth, mortality and yield per recruit for the spiny lobster, *Panulirus argus*, in St. Croix, USVI. Proceedings of the Gulf and Caribbean Fisheries Institute 53:58-75.

McGilliard, C., R. Hilborn, A. MacCall, A. Punt, and J. Field. 2010. Can information from marine protected areas be used to inform control-rule-based management of small scale, data-poor stocks? ICES Journal of Marine Science 68: 201-211.

Morgan L, L. Botsford, S. Wing, and B. Smith. 2000. Spatial variability in growth and mortality of the red sea urchin, *Strongylocentrotus franciscanus*, in northern California. Canadian Journal of Fisheries and Aquatic Sciences 57:980-992.

Mullon, C., P. Freon, and P. Curry. 2005. The dynamics of collapse in world fisheries. Fish and Fisheries 6:111-120.

NRC (National Research Council). 2004. Cooperative Research in the National Marine Fisheries Service. National Academies Press, Washington DC.

Orensanz, J., and G. Jamieson. 1998. The assessment and management of spatially structured stocks: an overview of the North Pacific Symposium on Invertebrate Stock Assessment and Management. Pp. 441-459 in: Proceedings of the North Pacific Symposium on Invertebrate Stock Assessment and Management, G.S. Jamieson and A. Campbell, Eds. Canadian Special Publication of Fisheries and Aquatic Sciences 125, NRC Research Press, Ottawa.

Prince, J. 2005. Combating the Tyranny of Scale for haliotids: Micro-management for Microstocks. Bulletin of Marine Science 76:557-578.

Prince, J., and R. Hilborn. 1998. Concentration profiles and invertebrate fisheries management. Pp. 187-196 in: Proceedings of the North Pacific Symposium on Invertebrate Stock Assessment and Management, G.S. Jamieson and A. Campbell, Eds. Canadian Special Publication of Fisheries and Aquatic Sciences 125, NRC Research Press, Ottawa.

Pringle, J. 1986. California spiny lobster (Panulirus interruptus) larval retention and recruitment: A review and synthesis. Canadian Journal of Fisheries and Aquatic Science 43:2142-2152.

Quinn, T., and R. Deriso. 1999. Quantitative Fish Dynamics. Oxford University Press, New York. 560 pp.

Taylor, B., and J. McIlwain. 2010. Beyond abundance and biomass: effects of marine protected areas on the demography of a highly exploited reef fish. Marine Ecology Progress Series 411:243-258.

Wilson, R. 1948. A review of the southern California spiny lobster fishery. California Fish and Game 34:71-80.

Wilson, J., J. Prince, and H. Lenihan. 2010. Setting harvest guidelines for sedentary nearshore species using marine protected areas as a reference. Marine and Coastal Fisheries: Dynamics, Management and Ecosystem Science 2:14-27.

Table 4.1. Mortality estimates for sites sampled across the three reserves in this study. Parameters *Z* and *F* are instantaneous total and fishing mortality, respectively. The parameters *a*, *m*, and, *u* are annualized rates of total mortality, natural mortality, and exploitation, respectively. The distance column represents the distance of sites from reserve borders (negative values are inside reserves, asterisks next to distance values denote the five sites used to estimate mean M described in text). All *Z* estimates are from Kay and Wilson *in review* (Chapter 3, this dissertation).

Site	Reserve	Dist. (m)	*Z*	*F*	*a*	*m*	*u*
Carrington Pt	Carr.	-3700*	0.039	-	0.038	0.165	-
Gull Island	Gull	-2250*	0.115	-	0.109	0.160	-
Punta Arena	Gull	-1850*	0.222	-	0.199	0.152	-
Grassy Knoll	Carr.	-1800*	0.148	-	0.137	0.157	-
Cavern Point	Scorp.	-1750*	0.322	-	0.275	0.145	-
Scorpion	Scorp.	-360	0.290	-	0.252	0.147	-
E. Morse Pt	Gull	-325	0.106	-	0.101	0.160	-
W. Morse Pt	Gull	-150	0.177	-	0.162	0.155	-
Border In	Carr.	-250	0.485	-	0.385	0.134	-
Border Out	Carr.	260	0.564	0.394	0.431	0.126	0.30
Little Scorpion	Scorp.	340	0.592	0.422	0.447	0.128	0.32
WMO	Gull	400	0.619	0.449	0.461	0.129	0.34
Far Out	Scorp.	1650	0.554	0.384	0.425	0.130	0.30
Rodes Reef	Carr.	2700	0.548	0.378	0.422	0.130	0.29
Brockway	Carr.	4700	0.546	0.376	0.421	0.130	0.29
Kinton	Gull	5200	0.692	0.522	0.499	0.122	0.38

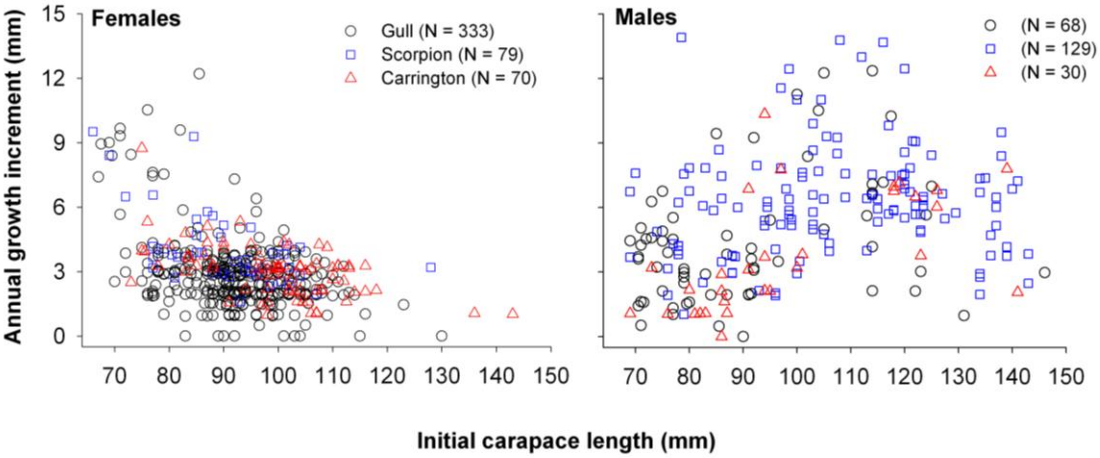

Figure 4.1. Growth increments (increase in carapace length, in mm) versus initial size at tagging for lobsters tagged and recaptured inside reserves during the 2006-2008 field seasons. Data reported here include only lobsters recaptured within 3 weeks of the anniversary of being tagged, and the growth increment for each individual was divided by the decimal years at liberty (e.g., 380 days at liberty = 1.041 years) such that increments reported are annual growth rates.

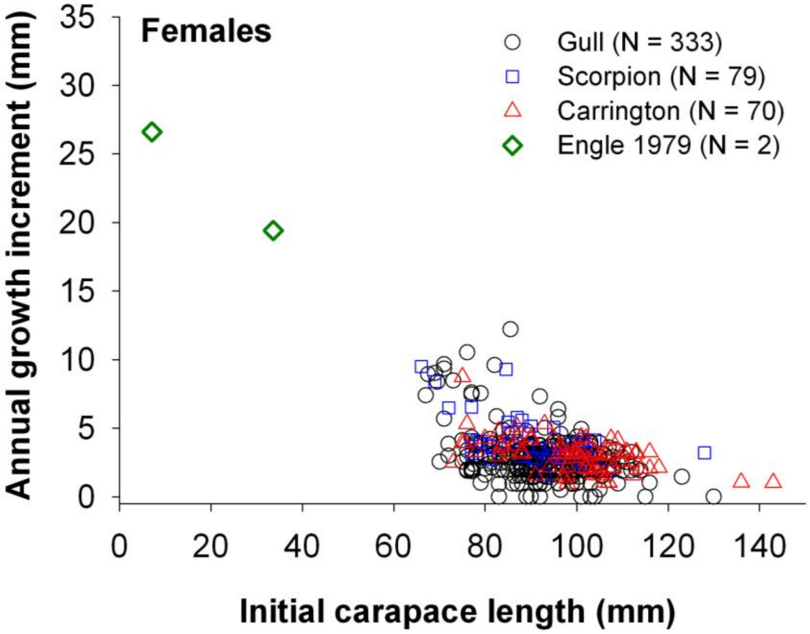

Figure 4.2. Female growth data reported in Figure 1, with growth increments for small juveniles included from Engel (1979). Engel data are included because traps used in my study did not consistently capture individuals smaller than ~70 mm. These are the data from which the VBGF parameters L_∞ and K were estimated.

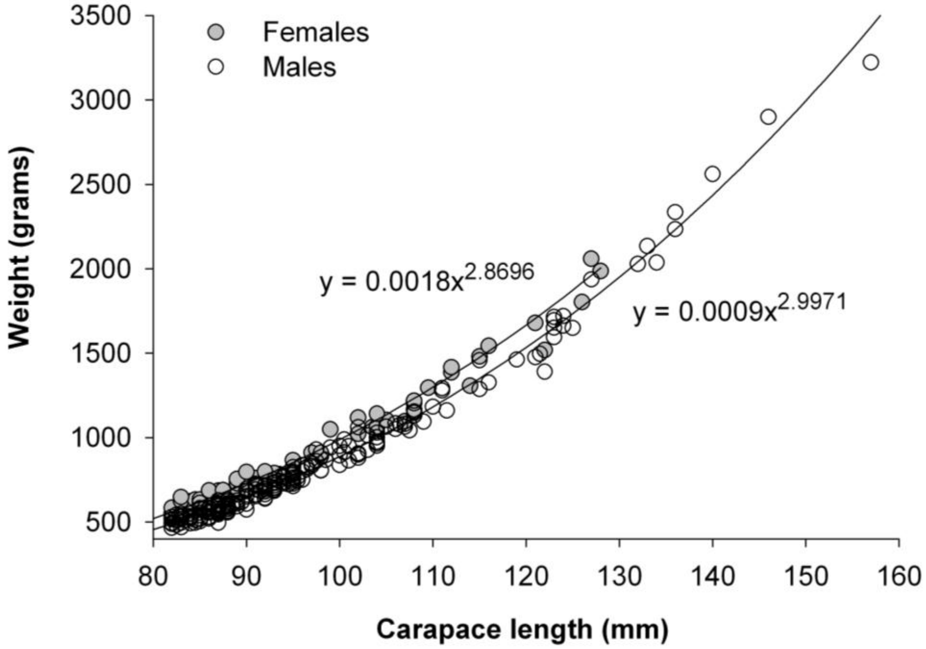

Figure 4.3. Length-weight relationships (and equations) for male and female lobsters measured during port sampling of commercial catch.

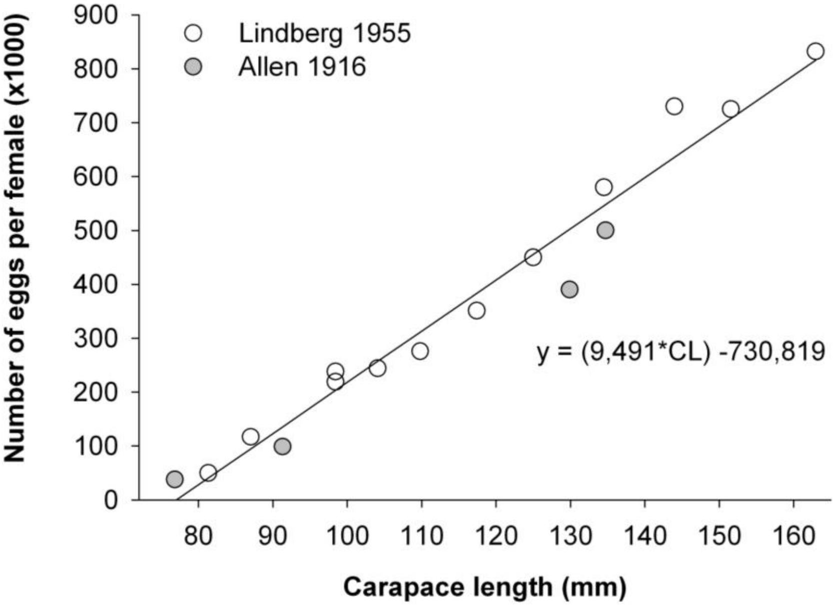

Figure 4.4. Best fit (using maximum likelihood) to fecundity data for *P. interruptus* reported by Allen (1916) and Lindberg (1955).

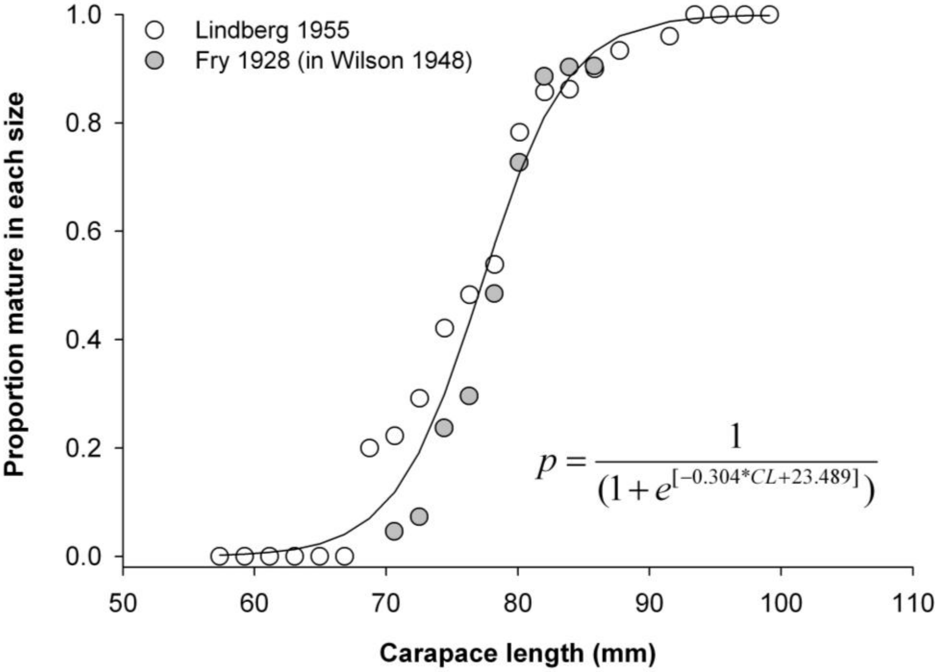

Figure 4.5. Size at maturity (SAM) for *P. interruptus*. Line and equation describe the best fit to data provided by Fry (1928, reported in Wilson 1948) and Lindberg (1955).

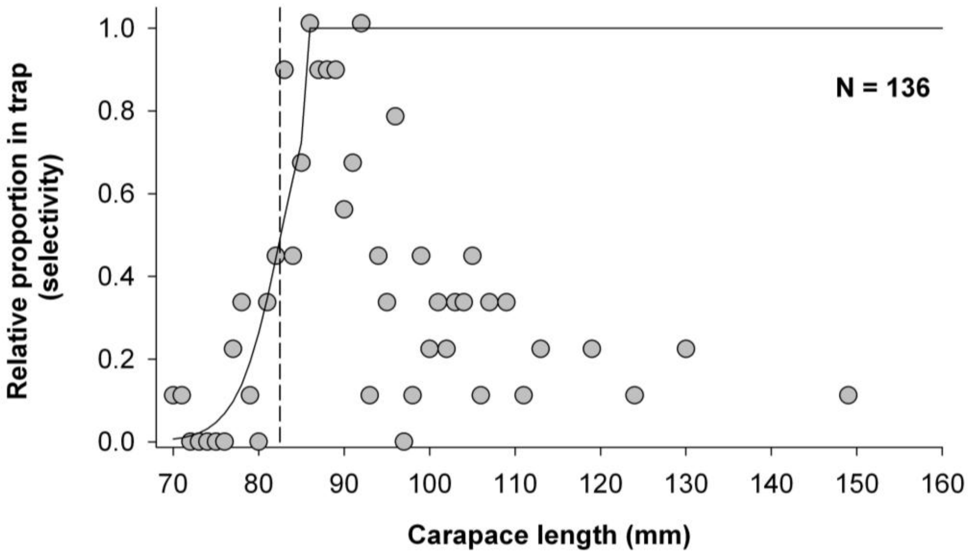

Figure 4.6. Relative proportion of different sized lobsters (1 mm size bins) trapped in standard commercial traps (i.e., with escape ports) deployed during research trapping. The solid line describes the best fit to the data for a modified logistic function. Dashed line is the minimum size limit (82.5 mm).

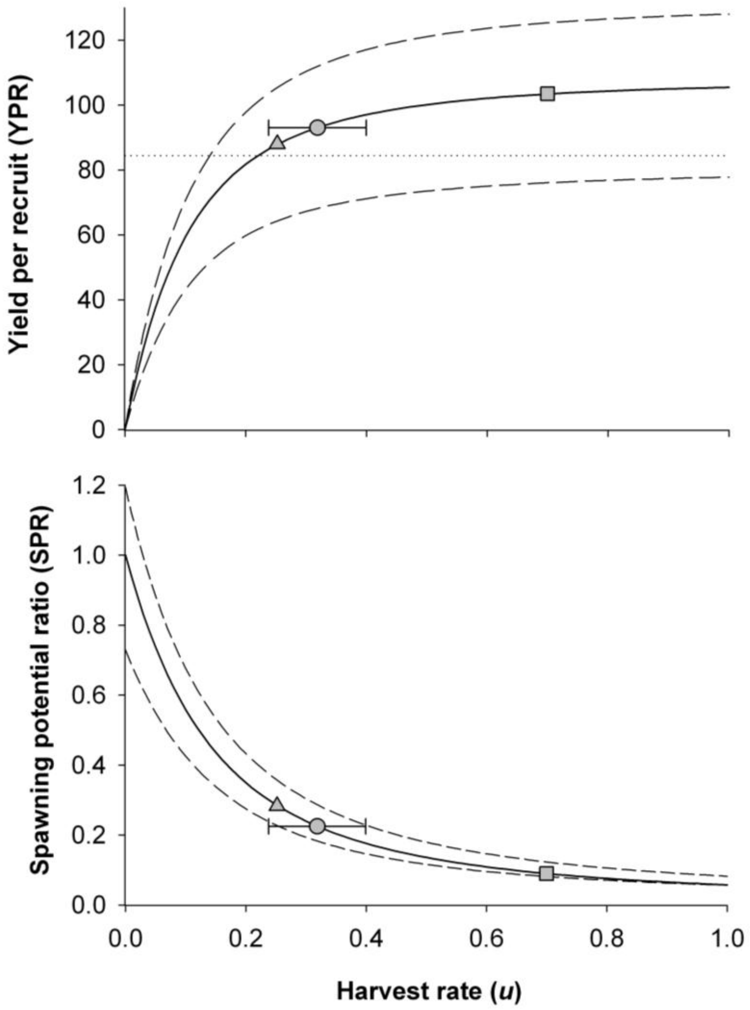

Figure 4.7. Yield per recruit (A) and spawning potential ratio (B) for *P. interruptus* across the range of all possible harvest rates (0-1). Dashed lines are 95% confidence intervals. Gray points and associated error bars are the grand mean and 95% confidence intervals for harvest rate (u) estimated across sites (see *Results* section).

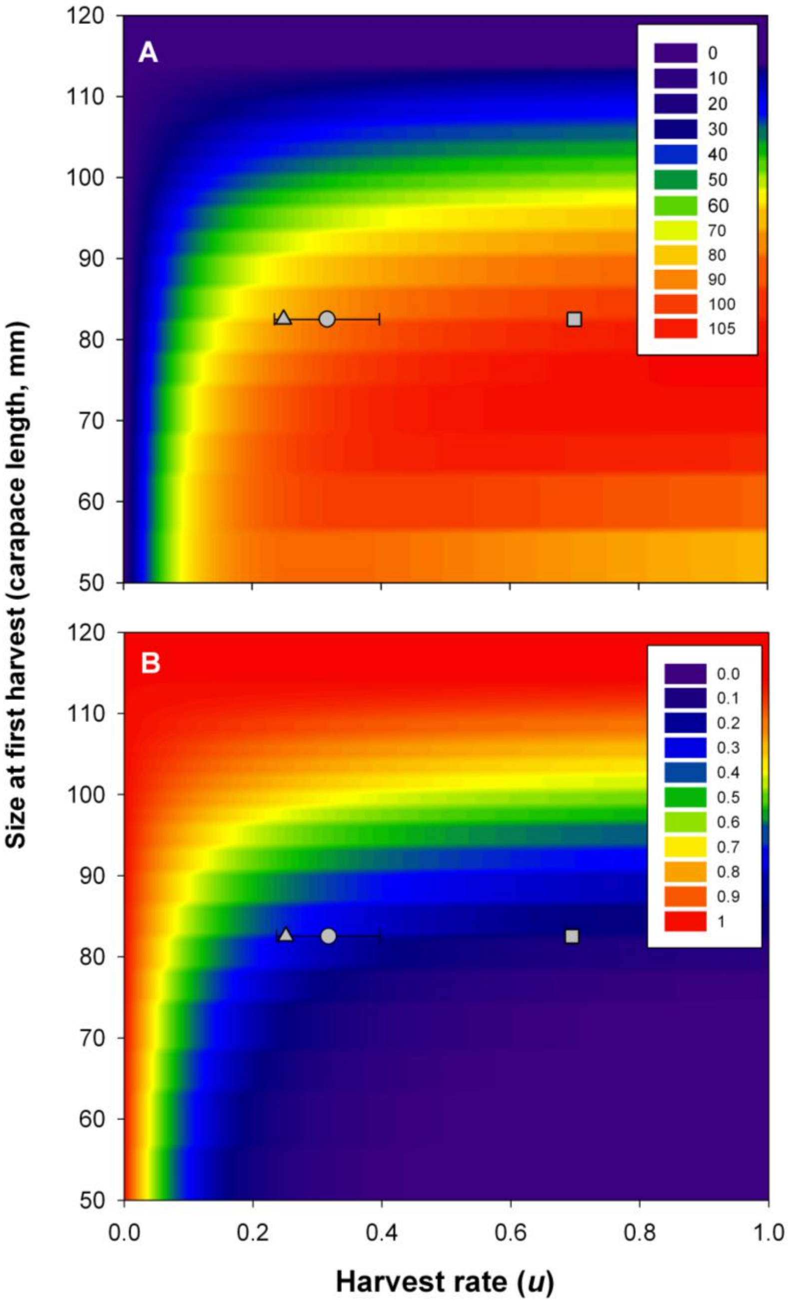

Figure 4.8. Yield per recruit (A) and spawning potential ratio (B) for *P. interruptus* across ranges of all possible harvest rates (0-1) and sizes at which lobsters are first harvested by the fishery. Gray points and associated error bars are the grand mean and 95% confidence intervals for harvest rate (u) estimated across sites (see *Results* section).