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Disentangling the effects of fishing and environmental forcing on demographic variation in an exploited species

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ABSTRACT

Species targeted by fishing often recover in abundance and size within marine protected areas (MPAs) resulting in increased reproductive potential. However, in some situations, concomitant changes in the abundance of predators, competitors, or prey within MPAs, or strong gradients in the surrounding environmental seascape may counteract the purported benefits making it more difficult to predict how species will respond to protection. We used a network of MPAs in California, spanning a large temperature gradient, to investigate the drivers of demographic variability in the commercially important red sea urchin *Mesocentrotus franciscanus*. We investigated how demographic metrics varied geographically in response to protection, temperature, and the main sea urchin resource, the giant kelp *Macrocystis pyrifera*. We found significant conservation benefits to this fished sea urchin within MPAs designated six years prior to the beginning of this study. Within MPAs, red sea urchins were generally larger resulting in greater adult biomass density and reproductive biomass density. In addition, kelp density was an important explanatory variable of all red sea urchin demographic traits examined (adult size, gonadosomatic index [GSI], density, adult biomass density, and reproductive biomass density). Kelp density was positively correlated with red sea urchin GSI and adult size, but the relationships with density, adult biomass density, and reproductive biomass density were complex and the directionality changed depending on the region (or environmental setting) examined. Our results demonstrate that kelp, red sea urchin reproduction, and the effects of spatial management on demographic processes are tightly coupled with the oceanographic regime.

1. Introduction

Understanding the ecological, environmental, and anthropogenic factors that control spatial variation in population demography allows for more accurate forecasting that can benefit resource management. Marine species are fished from wild populations that typically span broad spatial expanses over which biological traits of the species often vary. Biological variation in life history and demographic traits can occur in response to geographic or temporal shifts in temperature, productivity, resource availability, competition, and predation (including fishing pressure) (Bolnick et al., 2010; Bonel et al., 2013; Bonel and Lorda, 2015; Caselle et al., 2011; Castilla, 1999; Darimont et al., 2009; Dayton et al., 1998; Jackson et al., 2001; Lorda, 2014; Lorda and Lafferty, 2012; Menge, 2000; Menge and Sutherland, 1987; Paine, 1980; Polis and Hurd, 1996; Rogers-Bennett, 2007; Ruttenberg et al., 2005; Tegner and Dayton, 1981, 1977). While stock assessments have usually assumed that biological parameters such as growth, maturation or reproductive output are consistent across space, recent studies have shown that incorporating spatial variation in life histories into fisheries models and assessments can be useful for resource management (Beamish and Rothschild, 2009; Booth, 2000; Hamilton et al., 2011; Wilson et al., 2012, 2010; Worthington and Andrew, 1998). Understanding the drivers that may lead to spatial variation in key population

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parameters allows for better predictions concerning how species will respond in the future to changes that may result from climate change or new management regulations (Harley et al., 2006).

When fished predators increase within protected areas, such as in southern California, Australia, New Zealand, the Caribbean, the Mediterranean, and elsewhere, they can drive classic trophic cascades, resulting in lower densities of herbivores (Babcock et al., 2010, 1999; Barrett et al., 2009; Berriman et al., 2015; Harborne et al., 2009; Leleu et al., 2012; Ling et al., 2015; McClanahan, 2000; McClanahan et al., 2007; Micheli et al., 2005; Pederson and Johnson, 2006; Sala, 1997; Salomon et al., 2010; Shears and Babcock, 2003, 2002) even when they are targeted by fishing (Nichols et al., 2015; Shears et al., 2012). Thus, protection from fishing across all trophic levels may, in some cases, result in lower herbivore density and consequently lower recruitment. However, within an old marine protected area (MPA) at Anacapa Island, California red sea urchins may remain at population levels that are well above those at nearby unprotected sites, even in the long term (Behrens and Lafferty, 2004); the net gains from reduced fishing mortality are not entirely offset by increases in natural mortality.

Previous research has shown that reproduction of targeted species often is greater within MPAs. Species targeted by fishing activities frequently recover in density, size, and biomass inside well-designed MPAs (Babcock et al., 2010; Coleman et al., 2015; Lester et al., 2009; Ling and Johnson, 2012; Munguía-Vega et al., 2015) and reproductive output scales with biomass. While high levels of natural predation can reduce the reproductive output (Chesness et al., 1968; Durant, 2000; Magnhagen, 1991; Schwarzkopf and Shine, 1992) of targeted species by removing spawning biomass, harvesting by humans is different in that it often selects for larger and faster-growing individuals (i.e., the fittest individuals in the population). Harvesting wild species may result in lower reproductive rates than in adjacent non-harvested regions within many different global ecosystems, from terrestrial habitats (Hackney and McGraw, 2001; Novaro et al., 2000; Witkowski et al., 1994) to subtidal marine habitats (Beukers-Stewart et al., 2005). Reproductive potential is often higher within marine protected areas (MPAs) due to the presence of larger and older individuals (Allison et al., 1998; Gell and Roberts, 2003; Guidetti, 2006; Rogers-Bennett et al., 2002; Tetreault and Ambrose, 2007; Tuya et al., 2000; Wilson et al., 2014). Reproduction has also been shown to increase with greater resource availability (Claisse et al., 2013). However, spatial gradients in environmental conditions, such as temperature, may modify both resource availability and reproductive rates (Durant et al., 2007). Elevated temperatures can positively influence the reproductive capacity of invertebrates, yet depressed reproductive rates may occur above and below windows of optimal thermal tolerance (Bennett and Giese, 1955). While food quality and availability are hypothesized to be more important than temperature in driving variation in reproductive output (Brockington and Clarke, 2001), the relative importance of three major driving factors – protection from fishing, resource availability, and temperature – on the demography of a marine species is not entirely understood.

Sea urchins are important herbivores on temperate reefs that can cause widespread loss of kelp forests (Ling et al., 2015). In some regions, they also support important fisheries where they are harvested for their roe (Andrew et al., 2002). Sea urchins have been shown to decline in MPAs in some regions due to increases in previously fished predators (Shears and Babcock, 2003). However, harvested species of sea urchins may benefit directly from protection due to reduced harvest mortality (Quinn et al., 1993). Furthermore, reproductive potential of individual sea urchins is closely tied to food availability (Rogers-Bennett et al., 1995). Kelp is the major food source for sea urchins on many temperate reefs and kelp abundance is strongly influenced by oceanographic (Cavanaugh et al., 2011) and biotic factors such as urchin grazing (Ling et al., 2015), in addition to spatial management such as MPAs (Babcock et al., 2010; Lafferty, 2004). Consequently, predicting how sea urchin populations and their reproductive potential will be affected by protection is complicated and will likely vary across environmental and exploitation gradients.

A network of MPAs in the Northern Channel Islands in southern California offers an ideal setting for research focused on teasing apart the effects of environmental forcing on demographic variability in areas with and without fishing pressure. The Northern Channel Islands span a large gradient in temperature (Fig. 1), productivity, and wave exposure, that results in dramatic biogeographic variation in community composition over a small spatial scale (Blanchette et al., 2007; Hamilton et al., 2010; Harms and Winant, 1998). Eleven MPAs have been established around the 4 islands: the Anacapa Island State Marine Reserve (SMR) established in 1978 and ten additional MPAs established in 2003 (Hamilton et al., 2010). Previous studies within this region have documented changes in fish communities in response to the establishment of MPAs (Hamilton et al., 2010; Tetreault and Ambrose, 2007) and the recovery of fished predatory species such as spiny lobster and California sheephead wrasse within many of the MPAs (Caselle et al., 2015; Hamilton and Caselle, 2014; Kay et al., 2012). Within the long-established Anacapa Marine Reserve at the Northern Channel Islands, spiny lobster are thought to play an important role maintaining kelp forests by keeping purple sea urchin *Strongylocentrotus purpuratus* densities low (Lafferty, 2004; Shears et al., 2012). Purple urchins are not harvested and form extensive barrens areas in the warmer eastern part of the Channel Islands (Shears et al., 2012). The giant kelp (*Macrocystis pyrifera*, hereafter *kelp*) has been generally more abundant in the western region of the islands, largely due to cooler temperatures, higher nutrients, and a reduced frequency of urchin barrens (Behrens and Lafferty, 2004; Bell et al., 2015; Cavanaugh et al., 2011; Palacios et al., 2013; Zimmerman and Kremer, 1984).

The red sea urchin *Mesocentrotus franciscanus* (previously *Strongylocentrotus*) is heavily exploited as a commercial fishery across this biogeographically diverse region (Kalvass and Hendrix, 1997; Kalvass and Rogers-Bennett, 2004; Shears et al., 2012). More than half of California's red urchin landings (~5000 metric tons per annum) come from within the Northern Channel Islands (California Department of Fish and Wildlife [CDFW]). While there is extensive knowledge of the basic ecology of southern California marine subtidal ecosystems (Foster and Schiel, 2010; Graham, 2004; Shears et al., 2012; Tegner and Dayton, 2000), spatially-explicit patterns and drivers of variation in red sea urchin demographics remain poorly understood. Previous studies have reported greater size, biomass, and reproductive biomass of red sea urchins within the Anacapa MPA compared to adjacent fished sites (Behrens and Lafferty, 2004; Shears et al., 2012). Despite high predator densities in this MPA, moderate numbers of red sea urchins are able to persist, and due to their larger size, biomass is higher than at fished sites where large individuals are harvested. The Anacapa MPA is located in the warm eastern part of the Channel Islands, whereas the red sea urchin fishery is concentrated in the western part of the Channel Islands (Shears et al., 2012). It is therefore unknown how red sea urchin populations are affected by protection across the wider network of MPAs that span the Channel Islands. Here, we explore how red urchin population characteristics differ between MPA and fished sites across this large environmental gradient. We then examine how these patterns relate to variation in kelp density and temperature.

2. Methods

2.1. Biological surveys

To explore potential ecological factors associated with spatial variation in red sea urchin demographics, we conducted diver surveys of benthic kelp forest community structure throughout the four northern Channel Islands: Anacapa Island, Santa Cruz (SCI), Santa Rosa (SRI), and San Miguel Islands (SMI) (Fig. 1) during three northern-hemisphere summers (June–August in 2009 and 2011 and June–October in 2010). The sampling effort was a part of the Partnership for

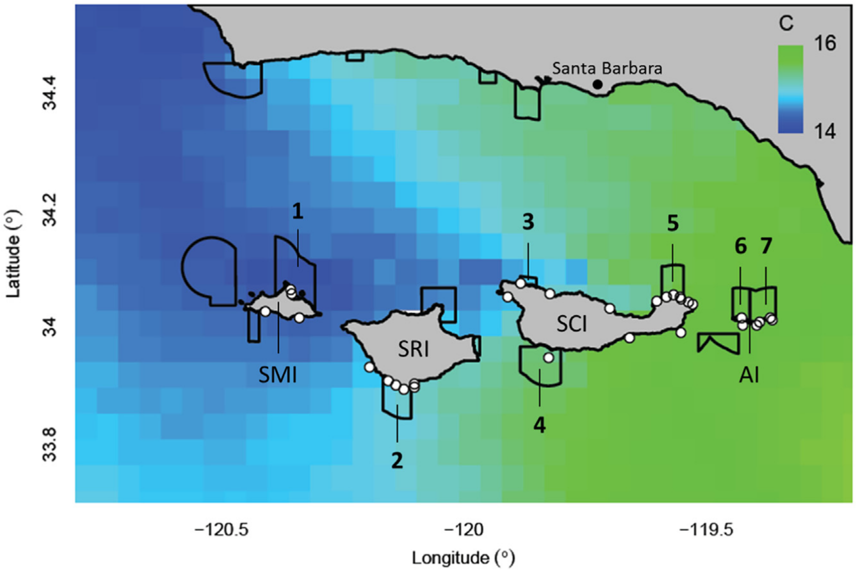

Fig. 1. Map of the Santa Barbara Channel and northern Channel Islands with sites (white dots) and mean long-term satellite sea surface temperatures (SST) represented by colors from blue to green (25-year average Advanced Very High Resolution Radiometer data from 1985 to 2009). All marine protected areas (MPAs) are outlined in black. The sites examined in this study are within seven MPAs (1) Harris Point State Marine Reserve (SMR), (2) South Point SMR, (3) Painted Cave State Marine Conservation Area (SMCA), (4) Gull Island SMR, (5) Scorpion SMR, (6) Anacapa Island SMCA, and (7) Anacapa Island SMR. Islands from west to east are shown: San Miguel Island (SMI), Santa Rosa Island (SRI), Santa Cruz Island (SCI), and Anacapa Island (AI). Twenty-five-year and one-year averages of SST are highly correlated with longitude ($r = 0.949$, $P < 0.0001$; $r = 0.959$, $P < 0.0001$, respectively).

Interdisciplinary Studies of Coastal Oceans' (PISCO) benthic subtidal monitoring program (Caselle et al., 2015; Hamilton et al., 2010).

We sampled from two depth zones (6 and 13 m) at an average of 11 sites within MPAs and 13 unprotected areas (open to fishing) per year across the northern Channel Islands ($n = 30$ unique sites across the three years). Although some sites were located within the same reef complex, sites were separated by at least 500 m and can be considered independent (Cavanaugh et al., 2014). We considered each sampling event ($n = 143$) as a separate replicate. Protected sites were located within seven MPAs (listed from west to east, Fig. 1): Harris Point State Marine Reserve (SMR), South Point SMR, Painted Cave State Marine Conservation Area (SMCA), Gull Island SMR, Scorpion SMR, Anacapa Island SMCA, and Anacapa Island SMR. Although recreational and commercial fishing of a limited number of species are allowed within the SMCAs, fishing for sea urchins is prohibited and thus SMCAs can be considered no-take marine reserves with respect to urchins. In comparison to unprotected areas, no-take marine reserves may have greater ecological differences than partially-protected conservation areas (Lester and Halpern, 2008), but we found no consistent urchin demographic differences between SMCAs and SMRs (see Appendix A for selected ecological patterns across all seven MPAs). Thus, all SMRs and SMCAs were categorized together (hereafter, *MPAs*) for the purposes of our analyses.

Divers recorded densities of red sea urchins >25 mm in test diameter along two 30 m × 2 m belt transects at each depth zone per site. To estimate sea urchin density, divers counted sea urchins within 10 m-segments along the belt transects. If divers counted 30 individuals before reaching the end of a 10-m segment, the length of the segment surveyed to that point was recorded, and densities of the entire 10 m segment were extrapolated (i.e., variable area subsampling). Within these transects, we counted the number of giant kelp plants and the number of stipes per plant (for all stipes >1 m in height) and summed the total stipes per square meter as our estimate of kelp density (i.e., kelp stipe density). For each site, density data for sea urchins and kelp were averaged across the two transects within the same depth zone.

Size-frequency data on red sea urchins were gathered through PISCO's program and the kelp forest monitoring program (KFMP) at the Channel Islands National Park (Kushner et al., 2013; Shears et al., 2012). We measured the first 150 urchins (comprehensively removing all urchins present in a given 2 m by 4 m swath until the desired number of urchins was reached) within a 50–100 m radius (depending on the density of urchins) of the PISCO transects that had already been sampled. For sites ($n = 19$) where PISCO did not collect size-frequency data, we used size-frequency data from nearby Channels Islands NPS KFMP sites using similar methods to the PISCO program.

2.2. Sea urchin collections for individual-based and population-based analyses

We investigated red sea urchin demographic metrics that are both ecologically important and relevant to the fishery. To examine individual urchin characteristics, we haphazardly collected adult red sea urchins ($n = 15–20$) per depth zone per site on each sampling date. We focused solely on adults >50 mm ($n = 2216$) because red sea urchins reach sexual maturity between about 51 and 76 mm (Tegner, 1989).

We examined two individual-based metrics of adult red sea urchin: *size* (test diameter) and *gonadosomatic index* (GSI), which is a strong metric of reproductive stage and value to the fishery (Unuma, 2002; Teck et al., 2017):

$$\mathrm{GSI} = \text{gonad wet weight [g]}/\text{total wet weight [g]} \qquad (1)$$

(i.e., the fraction of the organism mass that is gonad). We examined GSI separately for males and females.

To understand detailed regional variability in population-based characteristics of red sea urchins, we examined the patterns in: *density* (juvenile and adult individuals >25 mm per m^2), *adult biomass density*, and *reproductive biomass density* as a proxy for potential reproductive output. Biomass is a useful metric for assessing the population in both ecological and management terms. We examined adult biomass, since the fishery is based on harvesting adults (see Appendix B for information on juveniles and total biomass density). We first estimated the proportion of adult red sea urchins (>50 mm) per site for each year using size-frequency collections from PISCO or KFMP. To estimate adult red sea urchin density (for the adult biomass density metric), we multiplied the proportion of adult red sea urchins by the density (individuals >25 mm) per depth zone per site. Adult biomass per unit area within a site was estimated as:

$$\text{adult biomass density}\left[\mathrm{gm}^{-2}\right]=\text{adult density}\left[\text{individuals m}^{-2}\right] * \text{mean adult whole weight}\left[\mathrm{g/individual}\right]. \quad (2)$$

Reproductive biomass per unit area within a site was estimated as:

$$\begin{aligned}&\text{reproductive biomass density}\left[\mathrm{gm}^{-2}\right]\\&\quad=\text{adult density}\left[\text{individuals m}^{-2}\right]\\&\qquad * \text{mean gonad weight}\left[\mathrm{g/individual}\right].\end{aligned} \quad (3)$$

Previous estimates of biomass and reproductive biomass at sites within this region were based on density and size measurements at each site and estimated using known test-diameter to total weight and test-diameter to gonad weight relationships (Shears et al., 2012).

2.3. Environmental data

To examine the effect of spatial variation in temperature on red sea urchin demographics, we averaged satellite sea surface temperature (SST) records at each site from the previous year from the MODIS Terra and Aqua sensors (spg.ucsd.edu/Satellite_data/California_Current) at a 1-km spatial resolution (the closest pixel to each site). The data were daily images that were averaged into 15-day means (to minimize the cloud cover effect on any single day image) and then averaged across the prior year to each site's sampling date.

2.4. Data analyses

First, we described the geographic patterns of sea urchin demographic variables. Since the islands are oriented west to east (Fig. 1), the environmental gradient in temperature, productivity, and wave exposure is strongly correlated with longitude (Appendix C; $r = 0.949$, $P < 0.0001$; O'Reilly and Guza, 1993; Otero and Siegel, 2004). Thus, longitude is a convenient proxy for multiple interrelated environmental forcing variables. We used general linear models (GLMs) to examine how the sea urchin demographic variables (Table 1) changed as a function of protection from fishing, longitude, depth, and among years. We initially executed full-factorial designs for each model and then sequentially removed all non-significant interaction terms ($P > 0.05$).

Second, we examined the relative importance and interactions among three predictor variables (Table 1: protection from fishing [MPA versus unprotected area], mean kelp density, and mean sea surface temperature [over the previous year]) in driving red sea urchin demographics. We performed full-factorial GLMs for each of our five red sea urchin response variables (Table 1). All models were performed using JMP® 12.0.0, SAS Institute Inc. Transformations for predictor variables were performed to normalize the residuals of the models and are shown in Table 1. Since SMI contains a red sea urchin barren unique to the entire study region, we explored excluding sites within this island to identify effects of this anomalous area.

Preliminary analyses were conducted using DISTLM, where the best models are selected among all combinations of predictor variables using Akaike information criterion (Anderson et al., 2008). We decided not to pursue these methods, as they remove non-significant main effects, so comparing the relative importance of predictors among response variables would be impossible. However, we have included the results of those analyses in Appendix D as they complement the analyses of the GLMs.

Table 1
List of all variables, abbreviations, and their transformations for statistical models, if any.

Variable	Variable abbreviation	Transformation
Response variables:		
Mean red sea urchin (SU) gonadosomatic index	GSI	None
Mean adult red SU test diameter	TD	None
Mean red SU density	Density	ln (x + 1)
Mean adult red SU biomass density	Biomass	ln (x + 1)
Mean red SU reproductive biomass density	Reprod	ln (x + 1)
Predictor variables:		
Protection from fishing (MPA versus unprotected area)	MPA	Binary variable
Mean kelp stipe density	Kelp	ln (x + 1)
Mean sea surface temperature (over previous year)	SST	None

3. Results

3.1. Spatial and temporal variation in red sea urchin demography

3.1.1. Individual-based metrics: GSI and adult test diameter

There were no consistent spatial differences in GSI as a function of gender and thus males and females were pooled for further analyses (Appendix E). Sea urchins had higher GSI and were larger in the west (Table 2; Fig. 2; see Appendix F for results excluding SMI). On average red sea urchins had 28% higher GSI and were 14% larger at the two western islands than at the two eastern islands. For GSI there was a marginally significant interaction between MPA status and longitude, and GSI appeared to be greater at unprotected than protected sites in the west. However, this was largely driven by the very low GSI levels at the SMI MPA, which was dominated by a red sea urchin barren. There were no year-to-year differences in GSI.

Adult test diameter (TD) was on average 6% greater (5.2 mm) within MPAs across the region than at unprotected sites (Table 2; Fig. 2). In addition, there was a significant interaction between the east-west gradient (longitude) and depth; adult red sea urchins in the west were larger at deeper sites, but there was no clear relationship with adult size and depth in the east. Finally, adult red sea urchins were significantly larger in 2009 by on average 11 mm (88 mm) than in 2011 (77 mm), and were of intermediate size in 2010 (85 mm).

3.1.2. Population-based metrics: density, adult biomass density, and reproductive biomass density

Red sea urchin densities were highly variable across the region. There was a significant two-way interaction between longitude and year (Table 2; Fig. 3), with densities greater in the east in 2009. There was a significant interaction between longitude and protection from fishing with lower densities in fished areas in the west. In addition, within the west, densities were negatively related to depth.

Both adult red sea urchin biomass and reproductive biomass densities were significantly greater within MPA sites than unprotected sites (by 16% and 23%, respectively) and greater within shallower versus deeper sites (Table 2; Fig. 3). Reproductive biomass density also was significantly greater in the west than the east (on average red sea urchins had 9% higher reproductive biomass density at the two western islands than at the two eastern islands) (Table 2; Fig. 3). There were no year-to-year differences in biomass density and reproductive biomass density.

3.2. Drivers of red sea urchin demography

3.2.1. Individual-based metrics: GSI and adult test diameter

Kelp density was the strongest predictor of both GSI and size among sites (Table 3); sites with more kelp tended to have red sea urchins with greater GSI and of larger size (Fig. 4a and b). The positive relationship between kelp density and size was even stronger within MPAs than within unprotected sites (there was a

Table 2

General linear models examining spatial variability (year, longitude, protection from fishing, and depth) across individual-based and population-based response variables: red sea urchin gonadosomatic index (GSI), adult size (TD), density, adult biomass density, and reproductive biomass density: (a) overall model R^2, F-ratio, DF, and *P*-values and (b) effect tests. All non-significant interaction terms (indicated by a diagonal line in the table) were sequentially removed.

(a)

	Individual metrics		Population metrics		
Response variable	GSI	TD	Density	Biomass	Reprod
R^2	0.120	0.285	0.324	0.142	0.167
F-ratio$_{DF}$	$F_{6,142}$ 3.10	$F_{6,142}$ 9.02	$F_{9,142}$ 7.09	$F_{5,142}$ 4.54	$F_{5,142}$ 5.48
P	0.007	<0.0001	<0.0001	0.0007	0.0001

(b)

		Individual metrics						Population metrics								
		GSI			TD			Density			Biomass			Reprod		
Source	DF	F	*P*		F	*P*		F	*P*		F	*P*		F	*P*	
year	2	0.38	0.683		7.18	0.0011	**	0.45	0.6365		0.08	0.9222		0.16	0.8504	
long	1	9.99	0.0019	**	25.04	<0.0001	***	0.26	0.608		1.31	0.2543		6.82	0.01	*
Year* long	2							5.78	0.0039	**						
MPA	1	0.03	0.8619		9.70	0.0022	**	4.70	0.0319	*‡	13.20	0.0004	***	11.74	0.0008	***
Long* MPA	1	3.89	0.0507	†				7.54	0.0069	**						
depth	1	0.67	0.414		2.28	0.1335		31.49	<0.0001	***	9.25	0.0028	**	12.46	0.0006	***
Long* depth	1				6.37	0.0128	*‡	4.84	0.0295	*						

[a] marginally significant *P*-value.
[b] *P*-values were >0.05 when all interaction terms remained in the analysis.
**P* ≤0.05.
***P* ≤0.01.
****P* ≤0.001.

significant interaction between protection from fishing and kelp density) (Table 3; Fig. 4). The only other significant predictor of individual urchin characteristics was SST. Both red sea urchin size and GSI declined with increasing SST, following the longitudinal patterns described above.

3.2.2. Population-based metrics: density, adult biomass density, and reproductive biomass density

Red sea urchin density varied significantly across the islands, however the spatial patterns were complex due to a significant 3-way interaction among three factors: protection from fishing (MPA versus unprotected area), kelp density, and SST (Table 3; Fig. 4c). Kelp density was negatively related to red sea urchin density, but this relationship only occurred within protected areas in the western, cooler region, likely due to the protected site at SMI (Fig. 4c).

Protection from fishing was the strongest individual predictor of urchin adult biomass density (Table 3; Fig. 4d), with 16% higher biomass density within MPAs. In addition, there was a significant interaction between kelp density and SST, where adult biomass density within MPAs was positively associated with kelp density in the warmer (eastern) region and negatively associated with kelp density within the cooler (western) region (Fig. 4d).

Overall, reproductive biomass density was 23% greater within MPAs than in unprotected areas (Table 3; Figs. 3, 4e). In general, reproductive biomass density was positively related to kelp density and negatively related to SST. However, these two drivers interacted, with slightly higher levels of reproductive biomass density in areas with higher densities of kelp within the warmer and less fished eastern region (Fig. 4e), most evidently within MPAs. The opposite pattern occurred in the cooler (western) region (Fig. 4e), where reproductive biomass density declined with kelp density, similar to the pattern for adult biomass density.

3.2.3. Drivers of sea urchin demography excluding sites within SMI

If we exclude SMI from these analyses, kelp and SST are the only significant drivers of variation in red sea urchin adult density with no significant interactions. In addition, without sites in SMI, SST is no longer an important predictor of variation in GSI or reproductive biomass density but otherwise results are similar. Finally, drivers of TD and biomass density are statistically similar with the exclusion of SMI (Appendix F, Table F.2).

4. Discussion

We found that protection from fishing, kelp density, and temperature interact to explain the complexity of sea urchin demographics across the Channel Islands (see Table 4 for a summary of the key results). Although the majority of the MPAs within the region had only been designated six years prior to the beginning of this study, we detected significant differences in red sea urchin demographics between MPA and unprotected sites, highlighting the potential for conservation benefits. Kelp density was the most important direct driver of red sea urchin GSI and adult size and this factor was included in all the significant interaction terms in statistical models investigating the effects of protection from fishing and environmental forcing on red sea urchin population-based metrics. In addition, as described below, we found

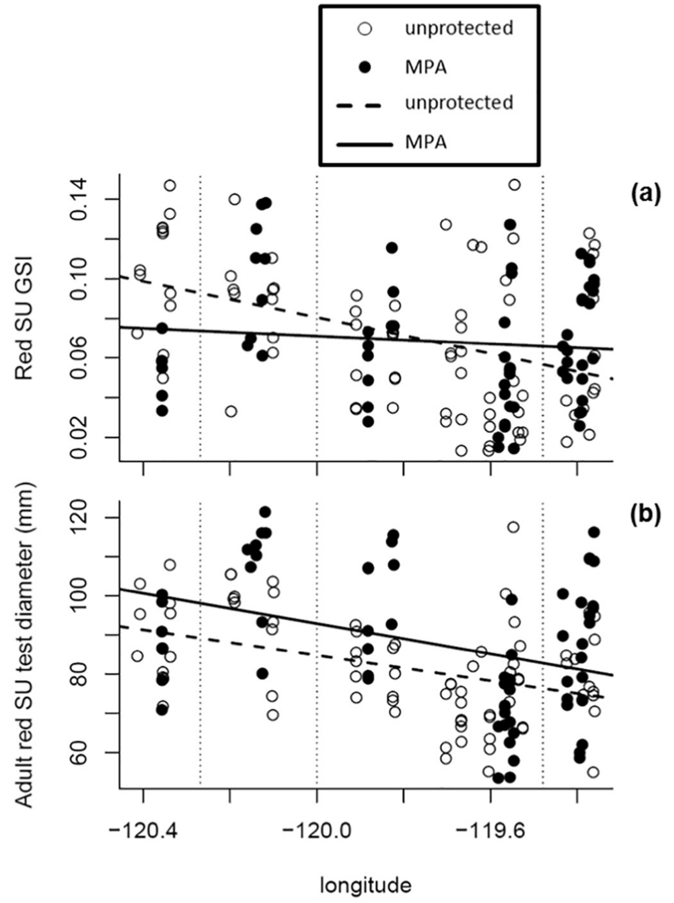

Fig. 2. Mean red sea urchin (SU) (a) gonadosomatic index (GSI) and (b) adult red SU test diameter (TD) per site per year across longitude from west to east (left to right) and grouped across MPA and unprotected areas. Vertical dotted lines separate the islands: San Miguel, Santa Rosa, Santa Cruz, and Anacapa Islands. Lines show linear regressions across longitude and between MPA and unprotected areas (GSI: $R^2 = 0.11$, $F_{3,142} = 5.92$, $P = 0.0008$; TD: $R^2 = 0.16$, $F_{3,142} = 9.08$, $P < 0.0001$).

several prominent regional differences in sea urchin demographics, which help explain the regional differences in fishing pressure and fishermen behavior across the northern Channel Islands (Shears et al., 2012).

Despite higher fishing mortality rates in the west (Shears et al., 2012; Teck et al., 2017), red sea urchins were still larger and had greater reproductive potential in the western (colder) region. This result is partially due to the enhanced primary productivity and greater kelp resource availability in the western region (Shears et al., 2012; Appendix G), and for many species, including red sea urchins, more food availability can result in higher reproductive output (Claisse et al., 2013). We not only detected greater total reproductive biomass density in western sites but also greater size-specific individual reproductive potential (GSI) in this region. Both reproductive measures were higher in the west, also partially due to the higher frequency of larger red sea urchins in this region. While some invertebrates typically senesce at a certain age and size, long-lived species may not show reductions in reproductive capacity; larger sea urchins typically have higher reproductive output and higher GSI than smaller conspecifics (Ebert, 2008; Gonor, 1972).

Furthermore, GSI was marginally significantly higher within unprotected western (colder) sites where kelp densities were significantly higher and purple sea urchin (*Strongylocentrotus purpuratus*) densities were lower (Appendix G). Purple sea urchins are prime space and resource competitors with red sea urchins (Dewees, 2003; Rogers-Bennett, 2007). More resource availability in the western region likely supports higher per-capita gonad growth; larger and heavier sea urchins found at western islands are consistent with this hypothesis (Ebert, 1968). In addition, the significantly lower values of many reproductive measures at MPAs compared to unprotected locations within the western (colder) region is partially due to a unique and persistent red urchin barren that formed at SMI (Harris Point) in years prior to the implementation of the MPA network (Kushner et al., 2013; Appendix A). This site supports the highest densities of red urchins at any of the sites examined in this study (8 ± 2.3 adults m^{-2} in comparison to the average across all sites of 2 ± 0.2 adults m^{-2}). The lower densities at nearby unprotected sites may reflect the heavy fishing pressure in this region (Teck et al., 2017) that alleviates resource competition for the remaining urchins.

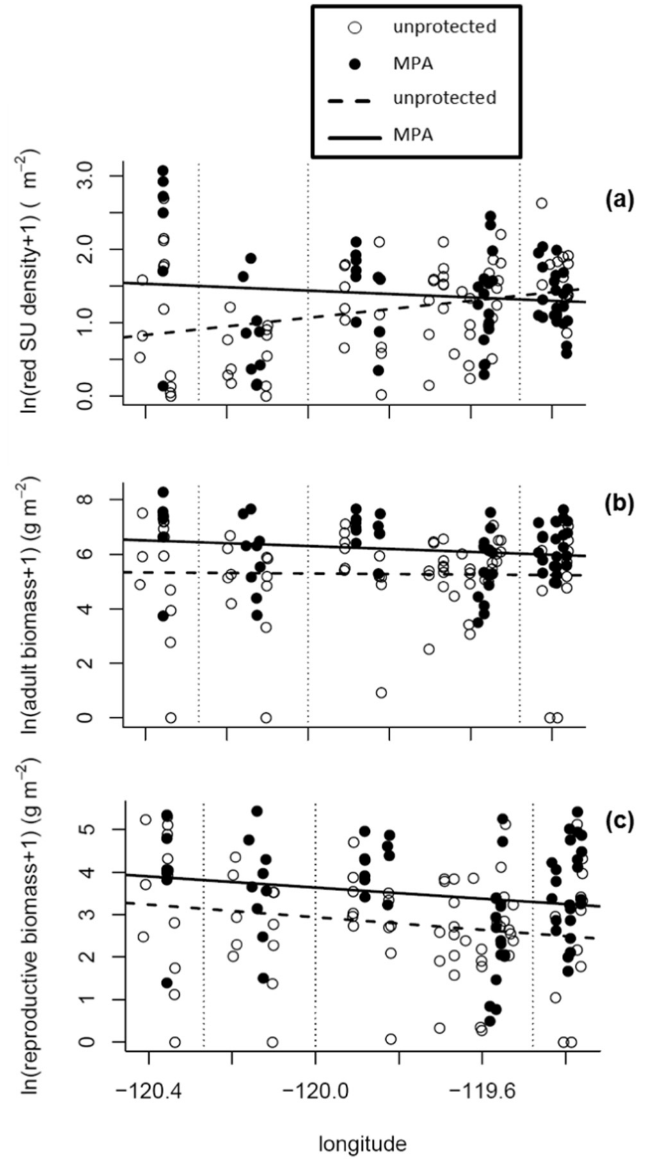

Fig. 3. Mean red sea urchin (SU) (a) density, (b) adult biomass density, and (c) reproductive biomass density (showing log-transformed values) across longitude from west to east (left to right) and grouped by MPA and unprotected areas. Vertical dotted lines separate the islands: San Miguel, Santa Rosa, Santa Cruz, and Anacapa Islands. Lines show linear regressions across longitude and between MPA and unprotected areas (density: $R^2 = 0.08$, $F_{3,142} = 3.80$, $P = 0.0118$; adult biomass density: $R^2 = 0.09$, $F_{3,142} = 4.33$, $P = 0.0060$; reproductive biomass density: $R^2 = 0.09$, $F_{3,142} = 4.56$, $P = 0.0044$).

Evidence from this study can help to explain the presence of a strong gradient in fishing pressure across the Channel Islands, with significantly higher red sea urchin landings in the west versus the east (Shears et al., 2012; Teck et al., 2017). In addition, our results showing lower

Table 3
General linear models examining spatial drivers (protection from fishing, kelp density, SST, and interactions) across individual-based and population-based response variables: red sea urchin GSI, adult TD, density, adult biomass density, reproductive biomass density: (a) overall model R^2, F-ratio, DF, and *P*-values and (b) effect tests.

(a)

	Individual metrics		Population metrics		
Response variable	GSI	TD	Density	Biomass	Reprod
R^2	0.459	0.430	0.262	0.163	0.259
F-ratio$_{7,142}$	16.35	14.53	6.84	3.75	6.73
P	<0.0001	<0.0001	<0.0001	0.001	<0.0001

(b)

		Individual metrics				Population metrics					
		GSI		TD		Density		Biomass		Reprod	
Source	DF	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*
MPA	1	0.1	0.7813	10.1	0.0018**	4.2	0.0415 *	10.8	0.0013**	10.8	0.0013**
Kelp	1	82.7	<0.0001***	55.8	<0.0001***	19.6	<0.0001***	0.0	0.8458	7.1	0.0085**
MPA ∗ kelp	1	1.7	0.1993	4.5	0.0002**	1.8	0.1816	0.2	0.6236	1.0	0.3226
SST	1	5.3	0.0229 *	13.7	0.0003**	0.5	0.4776	1.2	0.2668	4.2	0.0417*
MPA ∗ SST	1	1.1	0.3049	0.6	0.4218	2.7	0.0996	0.0	0.8578	0.2	0.6951
Kelp ∗ SST	1	0.3	0.5792	0.6	0.4548	4.6	0.0343*	8.3	0.0047**	10.9	0.0012**
MPA ∗ kelp ∗ SST	1	1.2	0.2798	0.4	0.5546	18.0	<0.0001***	2.2	0.1398	2.9	0.0887

* $P \le 0.05$.
** $P \le 0.01$.
*** $P \le 0.001$.

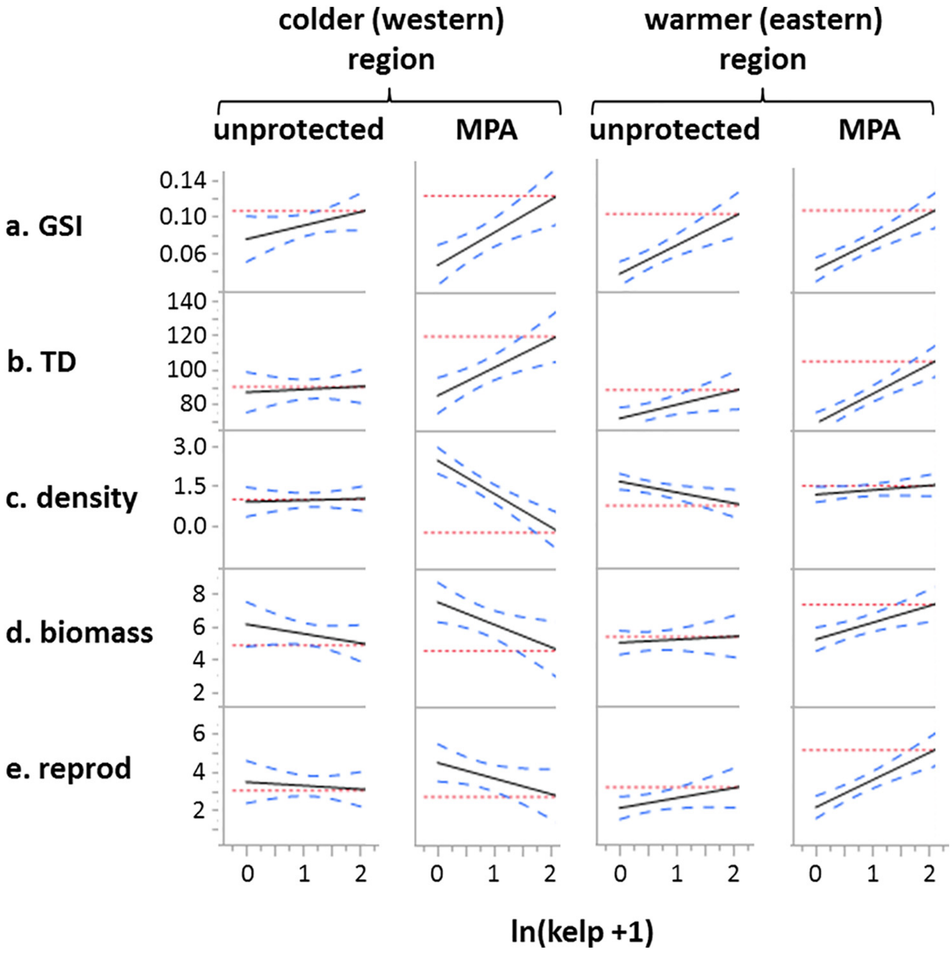

Fig. 4. Results from the GLMs examining spatial drivers (protection from fishing, kelp density, sea surface temperature [SST], and interactions) on urchin demographics. Figures depict the relationship between kelp density (m^{-2}) and each sea urchin demographic metric: (a) gonadosomatic index (GSI) and (b) adult test diameter (TD) (mm), (c) density (m^{-2}), (d) adult biomass density (>51 mm TD) ($g\,m^{-2}$), (e) reproductive biomass density ($g\,m^{-2}$) (reprod). The black lines show the predicted values of each metric across a range of kelp densities within the western region (left two columns) and the eastern region (right two columns) across both unprotected and MPA sites. The blue dashed lines show the 95% confidence intervals for the predicted values. Red dotted lines show the predicted values of each sea urchin demographic metric (horizontal lines) at the highest kelp density. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 4
Red sea urchin metrics across western (colder SST) and eastern (warmer SST) regions within the northern Channel Islands and MPAs versus unprotected areas (2009–2011). Unless otherwise noted, metrics refer to mean red sea urchin values.

Region status	Western region (colder)	Eastern region (warmer)	Entire region (colder or warmer)
MPA	** Densities higher (largely due to sites within Harris point SMR, SMI) *** Urchin density *negatively related* with kelp density (largely due to sites within Harris point SMR, SMI)		** Adult size larger ** Adult biomass density higher ** Reproductive biomass density higher ** Adult size *positively related* with kelp density
Unprotected	† GSI marginally higher (largely due to sites within Harris point SMR, SMI)		
MPA or Unprotected	* Adults larger and * Densities lower at deeper sites ** GSI higher * Reproductive biomass density higher ** Adult biomass density and reproductive biomass density *negatively related* with kelp density	** Densities higher in 2009 ** Adult biomass density and reproductive biomass density *positively related* with kelp density	** Adult biomass density and *** Adult reproductive biomass density higher at shallower sites ** Adult size in 2009 larger than in 2011 (intermediate in 2010) *** GSI *positively related* with kelp density * GSI and ** Adult size *negatively related* with SST

† Marginally significant P-value; *$P \leq 0.05$; **$P \leq 0.01$; ***$P \leq 0.001$.

densities in the west are consistent with the greater fishing pressure in the west, suggesting that fishing lowers density, as well as reduces size, biomass density, and reproductive biomass density. Partly due to the higher probability of finding larger red sea urchins in the west, the western region has been among the most productive regions for the commercial sea urchin fishery in recent decades (CDFW data [www.wildlife.ca.gov]). In addition, higher GSI is an indicator of superior gonad quality, which translates to higher prices (Kalvass and Hendrix, 1997; Unuma, 2002; Teck et al., 2017). We found that red sea urchins were larger with higher quality gonads in the western region, even though these sites experience consistently higher commercial fishing pressure (Teck et al., 2017).

Previous research has indicated that red sea urchin size structure and reproductive potential has benefitted from protection in the older MPA at Anacapa Island, which was established in 1978 (see Appendix H; Behrens and Lafferty, 2004; Shears et al., 2012). The newer MPAs of the Channel Islands network (established in 2003) are already showing similar trends in conservation benefits. On average adult red sea urchins were significantly larger (by 5.2 mm), had greater biomass density, and greater reproductive biomass density within MPA sites. Our findings corroborate previous research and catch data (CDFW) that show fishermen are removing large amounts of biomass density outside of MPAs and altering the size distributions by focusing harvest on sea urchins above the minimum size limit of 83 mm (Behrens and Lafferty, 2004).

In summary, protection from fishing was an important driver of red sea urchin density, adult size, biomass density, and reproductive biomass density. Adult red sea urchin size, biomass density, and reproductive biomass density were higher within protected areas versus unprotected areas. Protection from fishing was the most important predictor of population levels of adult biomass density, underlining effects of MPAs and fishing within this region. We found that kelp density was the most important driver of individual-based red sea urchin metrics: GSI and adult size. The positive relationship between kelp density and size was greater within MPAs than in unprotected sites, as these urchins are not removed by fishing. In addition, larger adult red sea urchins were associated with cooler temperatures in the west but were more strongly determined by regional differences in kelp density than temperature.

Sea surface temperature (SST) alone was not the most important predictor of any of the sea urchin metrics. However, there were significant interactions between SST and other predictors for all of our red sea urchin population-based metrics. In particular, kelp density was positively related to red sea urchin adult biomass density and reproductive biomass density, but only within the warmer (eastern) region. We thus found that regardless of temperature, there were significant differences in red sea urchin demographics across MPA and unprotected areas in the entire northern Channel Islands region (farthest right column of Table 4). Similarly, regardless of the level of protection from fishing, there were regional differences associated with variation in temperature (bottom row of Table 4). Through these investigations, we have been able to estimate the relative importance of these regional temperature differences, protection from fishing, and availability of resources on demographic variability in a fished species.

4.1. Implications

As we have shown here, the corresponding higher reproductive potential within MPAs can be a key benefit to species protection (Allison et al., 1998; Gell and Roberts, 2003; Tetreault and Ambrose, 2007) and may contribute to enhancing fisheries outside MPAs (Gaines et al., 2010; Rossetto et al., 2015). Despite this, in some situations the simple prediction that more protection leads to greater abundance, larger size, and greater reproductive potential of a fished species is not realized; other species may compensate for the reduced mortality from fishing via predation (Allison et al., 2003; Shears et al., 2012).

Both of our statistical models that tested (1) the importance of geographic proxies for environmental variables (i.e., longitude) or (2) specific environmental forcing variables (temperature and kelp abundance) on red sea urchin demographics, indicated that larger sizes, greater biomass density, and reproductive potential of red urchins occurred within MPAs versus unprotected areas. Although urchin predators have recovered to some extent within protected areas of this region (Caselle et al., 2015; Hamilton and Caselle, 2014; Kay et al., 2012), there were significant population-level responses by urchins to the elimination of fishing pressure. It remains to be seen whether these patterns will change as the predator populations continue to grow or individual predators achieve larger sizes. Besides potential community shifts from increasing lethal predator interactions with sea urchins, there is a rich body of evidence from previous research that non-lethal effects of predators are important in structuring communities (Lima, 1998; Madin et al., 2010; Scheibling and Hamm, 1991; Werner and Peacor, 2006, 2003). Prey respond to the presence of predators by avoidance (risk aversion) (Elner and Vadas, 1990; Madin et al., 2012) and reducing their foraging rates (Byrnes et al., 2006), and sea urchins clearly display these behaviors (Freeman, 2005). Thus, future research could address the relative roles of predation (by humans and other predators) and competition (mainly from the purple sea urchin, *Strongylocentrotus purpuratus*) as drivers of red sea urchin population dynamics.

While predation pressure is an important structuring force for herbivores and their algal prey in nearshore coastal waters (Hamilton and Caselle, 2014; Ling et al., 2015), our results underscore the significant impacts from humans as predators (Castilla, 1999; Darimont et al., 2009; Ling et al., 2009; Pinnegar et al., 2000) on herbivores that are themselves an important ecological engineer. Our results show that the alleviation of predation by humans through marine protected areas can benefit fished herbivores, but herbivore demographics are also tightly linked with macroalgal dynamics embedded in a complex thermal regime.

While no-take fishing areas may safeguard important macroalgal resources (Babcock et al., 2010; Lafferty, 2004), other proactive measures may be critical, such as performing restoration (Claisse et al., 2013) in areas of deforestation. Furthermore, it is well known that changes in the climate (i.e., temperature, pH, storm severity, and frequency) can have major impacts on marine ecosystems at various trophic levels and life stages (Gaitán-Espitia et al., 2014; Harley et al., 2006; Harvell et al., 2002; Hofmann et al., 2010; Hughes, 2000; Lafferty, 2009; McGowan et al., 1998; Mos et al., 2016; O'Donnell et al., 2010) which includes valuable species such as sea urchins. With climate models indicating an increase in the frequency and severity of storms (Easterling et al., 2000; Trenberth, 2012), research shows that kelp can be severely affected (Dayton et al., 1998; Dayton and Tegner, 1984; Gaitán-Espitia et al., 2014; Lafferty and Behrens, 2005; Reed et al., 2011) causing ecosystem-wide effects (Byrnes et al., 2011). In addition, warming temperatures and corresponding declines in nutrients may negatively affect kelp growth, and warmer temperatures will speed up urchin metabolic rates. Thus, urchins will potentially require more resources in a warmer environment with potentially less kelp available. Documenting changes in the ecosystem through monitoring programs is an important element of scientific research that should continue in regions where such programs exist and should start in other regions where there are data gaps.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.biocon.2017.03.014.

References

Allison, G.W., Lubchenco, J., Carr, M.H., 1998. Marine reserves are necessary but not sufficient for marine conservation. Ecol. Appl. 8:S79–S92. http://dx.doi.org/10.1890/1051-0761(1998)8[S79:MRANBN]2.0.CO;2.

Allison, G.W., Gaines, S.D., Lubchenco, J., Possingham, H.P., 2003. Ensuring persistence of marine reserves: catastrophes require adopting an insurance factor. Ecol. Appl. 13: S8–S24. http://dx.doi.org/10.1890/1051-0761(2003)013[0008:EPOMRC]2.0.CO;2.

Anderson, M.J., Gorley, R.N., Clarke, K.R., 2008. PERMANOVA + for PRIMER: Guide to Software and Statistical Methods PRIMER-E. pp. 1–214.

Andrew, N.L., Agatsuma, Y., Ballesteros, E., Bazhin, A.G., Creaser, E.P., Barnes, D.K.A., Botsford, L.W., Bradbury, A., Campbell, A., Dixon, J.D., Einarsson, S., Gerring, P.K., Hebert, K., Hunter, M., Hur, S.B., Johnson, C.R., Juinio-Meñez, M.A., Kalvass, P., Miller, R.J., Moreno, C.A., Palleiro, J.S., Rivas, D., Robinson, S.M.L., Schroeter, S.C., Steneck, R.S., Vadas, R.L., Woodby, D.A., Xiaoqi, Z., 2002. Status and management of world sea urchin fisheries. Oceanogr. Mar. Biol. Annu. Rev. 40, 343–425.

Babcock, R.C., Kelly, S., Shears, N.T., Walker, J.W., Willis, T.J., 1999. Changes in community structure in temperate marine reserves. Mar. Ecol. Prog. Ser. 189:125–134. http://dx.doi.org/10.3354/meps189125.

Babcock, R.C., Shears, N.T., Alcala, A.C., Barrett, N.S., Edgar, G.J., Lafferty, K.D., McClanahan, T.R., Russ, G.R., 2010. Decadal trends in marine reserves reveal differential rates of change in direct and indirect effects. Proc. Natl. Acad. Sci. U. S. A. 107: 18256–18261. http://dx.doi.org/10.1073/pnas.0908012107.

Barrett, N.S., Buxton, C.D., Edgar, G.J., 2009. Changes in invertebrate and macroalgal populations in Tasmanian marine reserves in the decade following protection. J. Exp. Mar. Biol. Ecol. 370:104–119. http://dx.doi.org/10.1016/j.jembe.2008.12.005.

Beamish, R.J., Rothschild, B.J., 2009. Accounting for spatial population structure in stock assessment: past, present, and future. In: Beamish, R.J., Rothschild, B.J. (Eds.), The Future of Fisheries Science in North America. Springer, Netherlands:pp. 405–426 http://dx.doi.org/10.1007/978-1-4020-9210-7.

Behrens, M.D., Lafferty, K.D., 2004. Effects of marine reserves and urchin disease on southern Californian rocky reef communities. Mar. Ecol. Prog. Ser. 279:129–139. http://dx.doi.org/10.3354/meps279129.

Bell, T.W., Cavanaugh, K.C., Reed, D.C., Siegel, D.A., 2015. Geographical variability in the controls of giant kelp biomass dynamics. J. Biogeogr. 42:2010–2021. http://dx.doi.org/10.1111/jbi.12550.

Bennett, J., Giese, A.C., 1955. The annual reproductive and nutritional cycles in two western sea urchins. Biol. Bull. 109:226–237. http://dx.doi.org/10.2307/1538723.

Berriman, J.S., Kay, M.C., Reed, D.C., Rassweiler, A., Goldstein, D.A., Wright, W.G., 2015. Shifts in attack behavior of an important kelp forest predator within marine reserves. Mar. Ecol. Prog. Ser. 522:193–201. http://dx.doi.org/10.3354/meps11157.

Beukers-Stewart, B.D., Vause, B.J., Mosley, M.W.J., Rossetti, H.L., Brand, A.R., 2005. Benefits of closed area protection for a population of scallops. Mar. Ecol. Prog. Ser. 298: 189–204. http://dx.doi.org/10.3354/meps298189.

Blanchette, C.A., Helmuth, B., Gaines, S.D., 2007. Spatial patterns of growth in the mussel, *Mytilus californianus*, across a major oceanographic and biogeographic boundary at Point Conception, California, USA. J. Exp. Mar. Biol. Ecol. 340:126–148. http://dx.doi.org/10.1016/j.jembe.2006.09.022.

Bolnick, D.I., Ingram, T., Stutz, W.E., Snowberg, L.K., Lau, O.L., Paull, J.S., 2010. Ecological release from interspecific competition leads to decoupled changes in population and individual niche width. Proc. R. Soc. B 277:1789–1797. http://dx.doi.org/10.1098/rspb.2010.0018.

Bonel, N., Lorda, J., 2015. Growth and body weight variability of the invasive mussel *Limnoperna fortunei* (Mytilidae) across habitat and season. Malacologia 58, 129–145.

Bonel, N., Solari, L.C., Lorda, J., 2013. Differences in density, shell allometry and growth between two populations of *Limnoperna fortunei* (Mytilidae) from the Río de La Plata Basin, Argentina. Malacologia 56:43–58. http://dx.doi.org/10.4002/040.056.0203.

Booth, A.J., 2000. Incorporating the spatial component of fisheries data into stock assessment models. ICES J. Mar. Sci. 57:858–865. http://dx.doi.org/10.1006/jmsc.2000.0816.

Brockington, S., Clarke, A., 2001. The relative influence of temperature and food on the metabolism of a marine invertebrate. J. Exp. Mar. Biol. Ecol. 258:87–99. http://dx.doi.org/10.1016/s0022-0981(00)00347-6.

Byrnes, J., Stachowicz, J.J., Hultgren, K.M., Hughes, A.R., Olyarnik, S.V., Thornber, C.S., 2006. Predator diversity strengthens trophic cascades in kelp forests by modifying herbivore behaviour. Ecol. Lett. 9, 61–71.

Byrnes, J.E., Reed, D.C., Cardinale, B.J., Cavanaugh, K.C., Holbrook, S.J., Schmitt, R.J., 2011. Climate-driven increases in storm frequency simplify kelp forest food webs. Glob. Chang. Biol. 17:2513–2524. http://dx.doi.org/10.1111/j.1365-2486.2011.02409.x.

Caselle, J.E., Hamilton, S.L., Schroeder, D.M., Love, M.S., Standish, J.D., Rosales-Casián, J.A., Sosa-Nishizaki, O., 2011. Geographic variation in density, demography, and life history traits of a harvested, sex-changing, temperate reef fish. Can. J. Fish. Aquat. Sci. 68: 288–303. http://dx.doi.org/10.1139/F10-140.

Caselle, J.E., Rassweiler, A., Hamilton, S.L., Warner, R.R., 2015. Recovery trajectories of kelp forest animals are rapid yet spatially variable across a network of temperate marine protected areas. Sci. Rep. 5:14102. http://dx.doi.org/10.1038/srep14102.

Castilla, J.C., 1999. Coastal marine communities: trends and perspectives from human-exclusion experiments. Trends Ecol. Evol. 14:280–283. http://dx.doi.org/10.1016/S0169-5347(99)01602-X.

Cavanaugh, K.C., Siegel, D.A., Reed, D.C., Dennison, P.E., 2011. Environmental controls of giant-kelp biomass in the Santa Barbara Channel, California. Mar. Ecol. Prog. Ser. 429:1–17. http://dx.doi.org/10.3354/meps09141.

Cavanaugh, K.C., Siegel, D.A., Raimondi, P.T., Alberto, F., 2014. Patch definition in metapopulation analysis: a graph theory approach to solve the mega-patch problem. Ecology 95:316–328. http://dx.doi.org/10.1890/13-0221.1.

Chesness, R.A., Nelson, M.M., Longley, W.H., 1968. The effect of predator removal on pheasant reproductive success. J. Wildl. Manag. 32, 683–697.

Claisse, J.T., Williams, J.P., Ford, T., Pondella II, D.J., Meux, B., Protopapadakis, L., 2013. Kelp forest habitat restoration has the potential to increase sea urchin gonad biomass. Ecosphere 4:38. http://dx.doi.org/10.1890/ES12-00408.1.

Coleman, M.A., Bates, A.E., Stuart-Smith, R.D., Malcolm, H.A., Harasti, D., Jordan, A., Knott, N.A., Edgar, G.J., Kelaher, B.P., 2015. Functional traits reveal early responses in marine reserves following protection from fishing. Divers. Distrib. 21:876–887. http://dx.doi.org/10.1111/ddi.12309.

Darimont, C.T., Carlson, S.M., Kinnison, M.T., Paquet, P.C., Reimchen, T.E., Wilmers, C.C., 2009. Human predators outpace other agents of trait change in the wild. Proc. Natl. Acad. Sci. U. S. A. 106:952–954. http://dx.doi.org/10.1073/pnas.0809235106.

Dayton, P.K., Tegner, M., 1984. Catastrophic storms, El Niño, and patch stability in a southern California kelp community. Science 224:283–285. http://dx.doi.org/10.1126/science.224.4646.283.

Dayton, P.K., Tegner, M.J., Edwards, P.B., Riser, K.L., 1998. Sliding baselines, ghosts, and reduced expectations in kelp forest communities. Ecol. Appl. 8, 309–322.

Dewees, C.M., 2003. Sea urchin fisheries: a California perspective. In: Lawrence, J.M., Guzman, O. (Eds.), Sea Urchins: Fisheries and Ecology. DEStech Pubs, Lancaster, PA, pp. 37–55.

Durant, S.M., 2000. Predator avoidance, breeding experience and reproductive success in endangered cheetahs, *Acinonyx jubatus*. Anim. Behav. 60:121–130. http://dx.doi.org/10.1006/anbe.2000.1433.

Durant, J.M., Hjermann, D.O., Ottersen, G., Stenseth, N.C., 2007. Climate and the match or mismatch between predator requirements and resource availability. Clim. Res. 33: 271–283. http://dx.doi.org/10.3354/cr033271.

Easterling, D.R., Meehl, G.A., Parmesan, C., Changnon, S.A., Karl, T.R., Mearns, L.O., 2000. Climate extremes: observations, modeling, and impacts. Science 289:2068–2074. http://dx.doi.org/10.1126/science.289.5487.2068.

Ebert, T.A., 1968. Growth rates of the sea urchin *Strongylocentrotus purpuratus* related to food availability and spine abrasion. Ecology 49:1075–1091. http://dx.doi.org/10.2307/1934491.

Ebert, T.A., 2008. Longevity and lack of senescence in the red sea urchin *Strongylocentrotus franciscanus*. Exp. Gerontol. 43:734–738. http://dx.doi.org/10.1016/j.exger.2008.04.015.

Elner, R.W., Vadas Sr., R.L., 1990. Inference in ecology: the sea urchin phenomenon in the Northwestern Atlantic. Am. Nat. 136, 108–125.

Foster, M.S., Schiel, D.R., 2010. Loss of predators and the collapse of southern California kelp forests (?): alternatives, explanations and generalizations. J. Exp. Mar. Biol. Ecol. 393:59–70. http://dx.doi.org/10.1016/j.jembe.2010.07.002.

Freeman, A., 2005. Size-dependent trait-mediated indirect interactions among sea urchin herbivores. Behav. Ecol. 17:182–187. http://dx.doi.org/10.1093/beheco/arj014.

Gaines, S.D., White, C., Carr, M.H., Palumbi, S.R., 2010. Designing marine reserve networks for both conservation and fisheries management. Proc. Natl. Acad. Sci. U. S. A. 107: 18286–18293. http://dx.doi.org/10.1073/pnas.0906473107.

Gaitán-Espitia, J.D., Hancock, J.R., Padilla-Gamiño, J.L., Rivest, E.B., Blanchette, C.A., Reed, D.C., Hofmann, G.E., 2014. Interactive effects of elevated temperature and pCO_2 on early-life-history stages of the giant kelp *Macrocystis pyrifera*. J. Exp. Mar. Biol. Ecol. 457:51–58 http://dx.doi.org/10.1016/j.jembe.2014.03.018.

Gell, F.R., Roberts, C.M., 2003. Benefits beyond boundaries: the fishery effects of marine reserves. Trends Ecol. Evol. 18:448–455. http://dx.doi.org/10.1016/S0169-5347(03)00189-7.

Gonor, J.J., 1972. Gonad growth in the sea urchin, *Strongylocentrotus purpuratus* (Stimpson) (echinodermata: Echinoidea) and the assumptions of gonad index methods. J. Exp. Mar. Biol. Ecol. 10:89–103. http://dx.doi.org/10.1016/0022-0981(72)90095-0.

Graham, M.H., 2004. Effects of local deforestation on the diversity and structure of southern California giant kelp forest food webs. Ecosystems 7:341–357. http://dx.doi.org/10.1007/s10021-003-0245-6.

Guidetti, P., 2006. Marine reserves reestablish lost predatory interactions and cause community changes in rocky reefs. Ecol. Appl. 16:963–976. http://dx.doi.org/10.1890/1051-0761(2006)016[0963:MRRLPI]2.0.CO;2.

Hackney, E.E., McGraw, J.B., 2001. Experimental demonstration of an Allee effect in American ginseng. Conserv. Biol. 15:129–136. http://dx.doi.org/10.1046/j.1523-1739.2001.98546.x.

Hamilton, S.L., Caselle, J.E., 2014. Exploitation and recovery of a sea urchin predator has implications for the resilience of southern California kelp forests. Proc. Biol. Sci. 282:20141817. http://dx.doi.org/10.1098/rspb.2014.1817.

Hamilton, S.L., Caselle, J.E., Malone, D.P., Carr, M.H., 2010. Incorporating biogeography into evaluations of the Channel Islands marine reserve network. Proc. Natl. Acad. Sci. U. S. A. 107:18272–18277. http://dx.doi.org/10.1073/pnas.0908091107.

Hamilton, S.L., Wilson, J.R., Ben-Horin, T., Caselle, J.E., 2011. Utilizing spatial demographic and life history variation to optimize sustainable yield of a temperate sex-changing fish. PLoS One 6, e24580. http://dx.doi.org/10.1371/journal.pone.0024580.

Harborne, A.R., Renaud, P.G., Tyler, E.H.M., Mumby, P.J., 2009. Reduced density of the herbivorous urchin *Diadema antillarum* inside a Caribbean marine reserve linked to increased predation pressure by fishes. Coral Reefs 28:783–791. http://dx.doi.org/10.1007/s00338-009-0516-6.

Harley, C.D.G., Hughes, A.R., Hultgren, K.M., Miner, B.G., Sorte, C.J.B., Thornber, C.S., Rodriguez, L.F., Tomanek, L., Williams, S.L., 2006. The impacts of climate change in coastal marine systems. Ecol. Lett. 9:228–241. http://dx.doi.org/10.1111/j.1461-0248.2005.00871.x.

Harms, S., Winant, C.D., 1998. Characteristic patterns of the circulation in the Santa Barbara Channel. J. Geophys. Res. 103:3041–3065. http://dx.doi.org/10.1029/97JC02393.

Harvell, C.D., Mitchell, C.E., Ward, J.R., Altizer, S., Dobson, A.P., Ostfeld, R.S., Samuel, M.D., 2002. Climate warming and disease risks for terrestrial and marine biota. Science 296:2158–2162. http://dx.doi.org/10.1126/science.1063699.

Hofmann, G.E., Barry, J.P., Edmunds, P.J., Gates, R.D., Hutchins, D.A., Klinger, T., Sewell, M.A., 2010. The effect of ocean acidification on calcifying organisms in marine ecosystems: an organism-to-ecosystem perspective. Annu. Rev. Ecol. Evol. Syst. 41: 127–147. http://dx.doi.org/10.1146/annurev.ecolsys.ll0308.120227.

Hughes, L., 2000. Biological consequences of global warming: is the signal already. Trends Ecol. Evol. 15:56–61. http://dx.doi.org/10.1111/j.1749-4877.2010.00200.x.

Jackson, J.B.C., Kirby, M.X., Berger, W.H., Bjorndal, K.A., Botsford, L.W., Bourque, B.J., Bradbury, R.H., Cooke, R., Erlandson, J., Estes, J.A., Hughes, T.P., Kidwell, S., Lange, C.B., Lenihan, H.S., Pandolfi, J.M., Peterson, C.H., Steneck, R.S., Tegner, M.J., Warner, R.R., 2001. Historical overfishing and the recent collapse of coastal ecosystems. 293, 629–638.

Kalvass, P.E., Hendrix, J.M., 1997. The California red sea urchin, *Strongylocentrotus franciscanus*, fishery: catch, effort, and management trends. Mar. Fish. Rev. 59, 1–17.

Kalvass, P.E., Rogers-Bennett, L., 2004. Annual Status of the Fisheries Report Through 2003. Report to the Fish and Game Commission as directed by the Marine Life Management Act of 1998 prepared by California Department of Fish and Game Marine Region. 9. pp. 1–14.

Kay, M.C., Lenihan, H.S., Guenther, C.M., Wilson, J.R., Miller, C.J., Shrout, S.W., 2012. Collaborative assessment of California spiny lobster population and fishery responses to a marine reserve network. Ecol. Appl. 22:322–335. http://dx.doi.org/10.1890/11-0155.1.

Kushner, D.J., Rassweiler, A., McLaughlin, J.P., Lafferty, K.D., 2013. A multi-decade time series of kelp forest community structure at the California Channel Islands. Ecology 94: 2655. http://dx.doi.org/10.1890/13-0562R.1.

Lafferty, K.D., 2004. Fishing for lobsters indirectly increases epidemics in sea urchins. Ecol. Appl. 14:1566–1573. http://dx.doi.org/10.1890/03-5088.

Lafferty, K.D., 2009. The ecology of climate change and infectious diseases. Ecology 90, 888–900.

Lafferty, K.D., Behrens, M.D., 2005. Temporal variation in the state of rocky reefs: does fishing increase the vulnerability of kelp forests to disturbance? In: Garcelon, D.K., Schwemm, C.A. (Eds.), Proceedings of the Sixth California Islands Symposium. National Park Service and Institute for Wildlife Studies, Ventura, CA, pp. 499–508

Leleu, K., Remy-Zephir, B., Grace, R., Costello, M.J., 2012. Mapping habitats in a marine reserve showed how a 30-year trophic cascade altered ecosystem structure. Biol. Conserv. 155:193–201. http://dx.doi.org/10.1016/j.biocon.2012.05.009.

Lester, S.E., Halpern, B.S., 2008. Biological responses in marine no-take reserves versus partially protected areas. Mar. Ecol. Prog. Ser. 367:49–56. http://dx.doi.org/10.3354/meps07599.

Lester, S.E., Halpern, B.S., Grorud-Colvert, K., Lubchenco, J., Ruttenberg, B.I., Gaines, S.D., Airamé, S., Warner, R.R., 2009. Biological effects within no-take marine reserves: a global synthesis. Mar. Ecol. Prog. Ser. 384:33–46. http://dx.doi.org/10.3354/meps08029.

Lima, S.L., 1998. Nonlethal effects in the ecology of predator-prey interactions: what are the ecological effects of anti-predator decision-making? Bioscience 48:25–34. http://dx.doi.org/10.2307/1313225.

Ling, S.D., Johnson, C.R., 2012. Marine reserves reduce risk of climate-driven phase shift by reinstating size and habitat specific trophic interactions. Ecol. Appl. 22:1232–1245. http://dx.doi.org/10.1890/11-1587.1.

Ling, S.D., Johnson, C.R., Frusher, S.D., Ridgway, K.R., 2009. Overfishing reduces resilience of kelp beds to climate-driven catastrophic phase shift. Proc. Natl. Acad. Sci. U. S. A. 106:22341–22345. http://dx.doi.org/10.1073/pnas.0907529106.

Ling, S.D., Scheibling, R.E., Rassweiler, A., Johnson, C.R., Shears, N., Connell, S.D., Salomon, A.K., Norderhaug, K.M., Pérez-Matus, A., Hernández, J.C., Clemente, S., Blamey, L.K., Hereu, B., Ballesteros, E., Sala, E., Garrabou, J., Cebrian, E., Zabala, M., Fujita, D., Johnson, L.E., 2015. Global regime shift dynamics of catastrophic sea urchin overgrazing. Philos. Trans. R. Soc. B 370:20130269. http://dx.doi.org/10.1098/rstb.2013.0269.

Lorda, J., 2014. The Distribution and Abundance of the California Horn Snail at Different Spatial Scales. (Ph.D. dissertation). University of California, Santa Barbara.

Lorda, J., Lafferty, K.D., 2012. Shading decreases the abundance of the herbivorous California horn snail, *Cerithidea californica*. J. Exp. Mar. Biol. Ecol. 432–433:148–155. http://dx.doi.org/10.1016/j.jembe.2012.07.009.

Madin, E.M.P., Gaines, S.D., Madin, J.S., Warner, R.R., 2010. Fishing indirectly structures macroalgal assemblages by altering herbivore behavior. Am. Nat. 176:785–801. http://dx.doi.org/10.1086/657039.

Madin, E.M.P., Gaines, S.D., Madin, J.S., Link, A.-K., Lubchenco, P.J., Selden, R.L., Warner, R.R., 2012. Do behavioral foraging responses of prey to predators function similarly in restored and pristine foodwebs? PLoS One 7, e32390. http://dx.doi.org/10.1371/journal.pone.0032390.

Magnhagen, C., 1991. Predation risk as a cost of reproduction. Trends Ecol. Evol. 6: 183–186. http://dx.doi.org/10.1016/0169-5347(91)90210-O.

McClanahan, T.R., 2000. Recovery of a coral reef keystone predator, *Balistapus undulatus*, in East African marine parks. Biol. Conserv. 94:191–198. http://dx.doi.org/10.1016/S0006-3207(99)00176-7.

McClanahan, T.R., Graham, N.A.J., Calnan, J.M., MacNeil, M.A., 2007. Toward pristine biomass: reef fish recovery in coral reef marine protected areas in Kenya. Ecol. Appl. 17:1055–1067. http://dx.doi.org/10.1890/06-1450.

McGowan, J.A., Cayan, D.R., Dorman, L.M., 1998. Climate-ocean variability and ecosystem response in the Northeast Pacific. Science 281:210–217. http://dx.doi.org/10.1126/science.281.5374.210.

Menge, B.A., 2000. Top-down and bottom-up community regulation in marine rocky intertidal habitats. J. Exp. Mar. Biol. Ecol. 250:257–289. http://dx.doi.org/10.1016/s0022-0981(00)00200-8.

Menge, B.A., Sutherland, J.P., 1987. Community regulation: Variation in disturbance, competition, and predation in relation to environmental stress and recruitment. Am. Nat. 130:730–757. http://dx.doi.org/10.1016/s0022-0981(00)00200-8.

Micheli, F., Benedetti-Cecchi, L., Gambaccini, S., Bertocci, I., Borsini, C., Osio, G.C., Romano, F., 2005. Cascading human impacts, marine protected areas, and the structure of Mediterranean reef assemblages. Ecol. Monogr. 75:81–102. http://dx.doi.org/10.1890/03-4058.

Mos, B., Byrne, M., Dworjanyn, S.A., 2016. Biogenic acidification reduces sea urchin gonad growth and increases susceptibility of aquaculture to ocean acidification. Mar. Environ. Res. 113:39–48. http://dx.doi.org/10.1016/j.quaint.2012.04.015.

Munguía-Vega, A., Sáenz-Arroyo, A., Greenley, A.P., Espinoza-Montes, J.A., Palumbi, S.R., Rossetto, M., Micheli, F., 2015. Marine reserves help preserve genetic diversity after impacts derived from climate variability: lessons from the pink abalone in Baja California. Glob. Ecol. Conserv. 4:264–276. http://dx.doi.org/10.1016/j.gecco.2015.07.005.

Nichols, K.D., Segui, L., Hovel, K.A., 2015. Effects of predators on sea urchin density and habitat use in a southern California kelp forest. Mar. Biol. 162:1227–1237. http://dx.doi.org/10.1007/s00227-015-2664-2.

Novaro, A.J., Redford, K.H., Bodmer, R.E., 2000. Effect of hunting in source-sink systems in the neotropics. Conserv. Biol. 14:713–721. http://dx.doi.org/10.1046/j.1523-1739.2000.98452.x.

O'Donnell, M.J., Todgham, A.E., Sewell, M.A., Hammond, L.M., Ruggiero, K., Fangue, N.A., Zippay, M.L., Hofmann, G.E., 2010. Ocean acidification alters skeletogenesis and gene expression in larval sea urchins. Mar. Ecol. Prog. Ser. 398:157–171. http://dx.doi.org/10.3354/meps08346.

O'Reilly, W.C., Guza, R.T., 1993. A comparison of two spectral wave models in the Southern California Bight. Coast. Eng. 19:263–282. http://dx.doi.org/10.1016/0378-3839(93)90032-4.

Otero, M.P., Siegel, D.A., 2004. Spatial and temporal characteristics of sediment plumes and phytoplankton blooms in the Santa Barbara Channel. Deep-Sea Res. II 51:1129–1149. http://dx.doi.org/10.1016/j.dsr2.2004.04.004.

Paine, R.T., 1980. Food webs: Linkage, interaction strength and community infrastructure. J. Anim. Ecol. 49:667–685. http://dx.doi.org/10.2307/4220.

Palacios, D.M., Hazen, E.L., Schroeder, I.D., Bograd, S.J., 2013. Modeling the temperature-nitrate relationship in the coastal upwelling domain of the California Current. J. Geophys. Res. Ocean. 118:3223–3239. http://dx.doi.org/10.1002/jgrc.20216.

Pederson, H.G., Johnson, C.R., 2006. Predation of the sea urchin *Heliocidaris erythrogramma* by rock lobsters (*Jasus edwardsii*) in no-take marine reserves. J. Exp. Mar. Biol. Ecol. 336:120–134. http://dx.doi.org/10.1016/j.jembe.2006.04.010.

Pinnegar, J.K., Polunin, N.V.C., Francour, P., Badalamenti, F., Chemello, R., Harmelin-Vivien, M.L., Hereu, B., Milazzo, M., Zabala, M., D'Anna, G., Pipitone, C., 2000. Trophic cascades in benthic marine ecosystems: lessons for fisheries and protected-area management. Environ. Conserv. 27:179–200. http://dx.doi.org/10.1017/S0376892900000205.

Polis, G.A., Hurd, S.D., 1996. Linking marine and terrestrial food webs: allochthonous input from the ocean supports high secondary productivity on small islands and coastal land communities. Am. Nat. 147:396–423. http://dx.doi.org/10.1086/285858.

Quinn, J.F., Wing, S.R., Botsford, L.W., 1993. Harvest refugia in marine invertebrate fisheries: models and applications to the red sea urchin, *Strongylocentrotus franciscanus*. Am. Zool. 33:537–550. http://dx.doi.org/10.1093/icb/33.6.537.

Reed, D.C., Rassweiler, A., Carr, M.H., Cavanaugh, K.C., Malone, D.P., Siegel, D.A., 2011. Wave disturbance overwhelms top-down and bottom-up control of primary production in California kelp forests. Ecology 92, 2108–2116.

Rogers-Bennett, L., 2007. The ecology of *Strongylocentrotus franciscanus* and *Strongylocentrotus purpuratus*. In: Lawrence, J.M. (Ed.), Edible Sea Urchins: Biology and Ecology. Elsevier, Amsterdam, pp. 393–425.

Rogers-Bennett, L., Bennett, W.A., Fastenau, H.C., Dewees, C.M., 1995. Spatial variation in red sea urchin reproduction and morphology: implications for harvest refugia. Ecol. Appl. 5:1171–1180. http://dx.doi.org/10.2307/2269364.

Rogers-Bennett, L., Haaker, P.L., Karpov, K.A., Kushner, D.J., 2002. Using spatially explicit data to evaluate marine protected areas for abalone in southern California. Conserv. Biol. 16, 1308–1317.

Rossetto, M., Micheli, F., Saenz-Arroyo, A., Espinoza-Montes, J., De Leo, G., 2015. No-take marine reserves can enhance population persistence and support the fishery of abalone. Can. J. Fish. Aquat. Sci. 72:1503–1517. http://dx.doi.org/10.1139/cjfas-2013-0623.

Ruttenberg, B.I., Haupt, A.J., Chiriboga, A.I., Warner, R.R., 2005. Patterns, causes and consequences of regional variation in the ecology and life history of a reef fish. Oecologia 145:394–403. http://dx.doi.org/10.1007/s00442-005-0150-0.

Sala, E., 1997. Fish predators and scavengers of the sea urchin *Paracentrotus lividus* in protected areas of the north-west Mediterranean Sea. Mar. Biol. 129:531–539. http://dx.doi.org/10.1007/s002270050194.

Salomon, A.K., Gaichas, S.K., Shears, N.T., Smith, J.E., Madin, E.M.P., Gaines, S.D., 2010. Key features and context-dependence of fishery-induced trophic cascades. Conserv. Biol. 24:382–394. http://dx.doi.org/10.1111/j.1523-1739.2009.01436.x.

Scheibling, R.E., Hamm, J., 1991. Interactions between sea urchins (*Strongylocentrotus droebachiensis*) and their predators in field and laboratory experiments. Mar. Biol. 110:105–116. http://dx.doi.org/10.1007/BF01313097.

Schwarzkopf, L., Shine, R., 1992. Costs of reproduction in lizards: escape tactics and susceptibility to predation. Behav. Ecol. Sociobiol. 31:17–25. http://dx.doi.org/10.1007/BF00167812.

Shears, N.T., Babcock, R.C., 2002. Marine reserves demonstrate top-down control of community structure on temperate reefs. Oecologia 132:131–142. http://dx.doi.org/10.1007/s00442-002-0920-x.

Shears, N.T., Babcock, R.C., 2003. Continuing trophic cascade effects after 25 years of no-take marine reserve protection. Mar. Ecol. Prog. Ser. 246:1–16. http://dx.doi.org/10.3354/meps246001.

Shears, N.T., Kushner, D.J., Katz, S.L., Gaines, S.D., 2012. Reconciling conflict between the direct and indirect effects of marine reserve protection. Environ. Conserv. 39:225–236. http://dx.doi.org/10.1017/S0376892912000082.

Teck, Sarah J., Lorda, Julio, Shears, Nick T., Ben-Horin, Tal, Toseland, Rebecca E., Rathbone, Sarah T., Gaines, Steven D., 2017. Quality of a fished resource: Assessing spatial and temporal dynamics. PLOS ONE (accepted for publication).

Tegner, M.J., 1989. The feasibility of enhancing red sea urchin, *Strongylocentrotus franciscanus*, stocks in California: an analysis of the options. Mar. Fish. Rev. 51, 1–22.

Tegner, M.J., Dayton, P.K., 1977. Sea urchin recruitment patterns and implications of commercial fishing. Science 196:324–326. http://dx.doi.org/10.1126/science.847476.

Tegner, M.J., Dayton, P.K., 1981. Population structure, recruitment and mortality of two sea urchins (*Strongylocentrotus franciscanus* and *S. purpuratus*) in a kelp forest. Mar. Ecol. Prog. Ser. 5:255–268. http://dx.doi.org/10.3354/meps005255.

Tegner, M.J., Dayton, P.K., 2000. Ecosystem effects of fishing in kelp forest communities. ICES J. Mar. Sci. 57:579–689. http://dx.doi.org/10.1006/jmsc.2000.0715.

Tetreault, I., Ambrose, R.F., 2007. Temperate marine reserves enhance targeted but not untargeted fishes in multiple no-take MPAs. Ecol. Appl. 17:2251–2267. http://dx.doi.org/10.1890/06-0161.1.

Trenberth, K.E., 2012. Framing the way to relate climate extremes to climate change. Clim. Chang. http://dx.doi.org/10.1007/s10584-012-0441-5.

Tuya, F.C., Soboil, M.L., Kido, J., 2000. An assessment of the effectiveness of marine protected areas in the San Juan Islands, Washington, USA. ICES J. Mar. Sci. 57:1218–1226. http://dx.doi.org/10.1006/jmsc.2000.0808.

Unuma, T., 2002. Gonadal growth and its relationship to aquaculture in sea urchins. In: Yokota, Y., Matranga, V., Smolenicka, Z. (Eds.), The Sea Urchin: From Basic Biology to Aquaculture. A.A. Balkema, Lisse, The Netherlands, pp. 115–128.

Werner, E.E., Peacor, S.D., 2003. A review of trait-mediated indirect interactions in ecological communities. Ecology 84, 1083–1100.

Werner, E.E., Peacor, S.D., 2006. Lethal and nonlethal predator effects on an herbivore guild mediated by system productivity. Ecology 87:347–361. http://dx.doi.org/10.1890/05-0091.

Wilson, J.R., Prince, J.D., Lenihan, H.S., 2010. A management strategy for sedentary nearshore species that uses marine protected areas as a reference. Mar. Coast. Fish. Dyn. Manag. Ecosyst. Sci. 2:14–27. http://dx.doi.org/10.1577/C08-026.1.

Wilson, J.R., Kay, M.C., Colgate, J., Qi, R., Lenihan, H.S., 2012. Small-scale spatial variation in population dynamics and fishermen response in a coastal marine fishery. PLoS One 7, e52837. http://dx.doi.org/10.1371/journal.pone.0052837.

Wilson, J.R., Valencia, S.R., Kay, M.C., Lenihan, H.S., 2014. Integration of no-take marine reserves in the assessment of data-limited fisheries. Conserv. Lett. 7:451–458. http://dx.doi.org/10.1111/conl.12073.

Witkowski, E.T.F., Lamont, B.B., Obbens, F.J., 1994. Commercial picking of *Banksia hookeriana* in the wild reduces subsequent shoot, flower and seed production. J. Appl. Ecol. 31:508–520. http://dx.doi.org/10.2307/2404446.

Worthington, D., Andrew, N., 1998. Small scale variation in demography and its implications for an alternative size limit in the fishery for blacklip abalone (*Haliotis rubra*) in New South Wales, Australia. In: Jamieson, G., Campbell, A. (Eds.), Proceedings of the North Pacific Symposium on Invertebrate Stock Assessment and Management. Can Spec Publ Fish Aquat Sci vol. 125, pp. 341–348.

Zimmerman, R.C., Kremer, J.N., 1984. Episodic nutrient supply to a kelp forest ecosystem in Southern California. J. Mar. Res. 42:591–604. http://dx.doi.org/10.1357/002224084788506031.