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Kelp forest habitat restoration has the potential to increase sea urchin gonad biomass

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Abstract. When taking an ecosystem-based approach to marine resource management, managers may be able to implement a combination of management tools in order to mitigate the socioeconomic impacts of implementing any one in isolation, while providing greater overall ecological benefits. The harvest of *Strongylocentrotus franciscanus* (red sea urchin) for their gonads is one of the most important commercial fisheries in California. However, in some locations, high densities of the unfished *Strongylocentrotus purpuratus* (purple sea urchin) can clear expanses of kelp forest resulting in "urchin barrens." The lack of macroalgal food resources can result in reduced gonad production, making *S. franciscanus* within barrens less valuable to a fishery. We investigated the potential of kelp forest habitat restoration, which may be achievable primarily by removing *S. purpuratus* from barrens, to positively impact the local *S. franciscanus* fishery and offset the losses in fishing grounds within recently established MPAs in our study area. Generalized linear modeling of the relationship between gonad weight and length (test diameter) demonstrated clear size-specific differences in gonad production between urchins collected in barrens and kelp forests. These relationships varied over time, with the maximum observed mean gonad biomass at length being 484% greater in kelp forest than barren habitat for *S. franciscanus* just above the legal size limit. The variability in *S. franciscanus* density (5.2 times greater in urchin barrens), size structure (mean test diameters were approximately 50% greater in kelp forest) and gonad production were then incorporated using Monte Carlo simulations. Results indicated that restoration could potentially result in an 864% increase in *S. franciscanus* gonad biomass available to the fishery, and a 132% increase in reproductive potential per unit area of urchin barren restored to kelp forest. If all 36 ha of urchin barren habitat mapped outside of the new MPAs in the study area were restored, the increase in gonad biomass available to the fishery could potentially offset 52% of which is now protected within the 109 ha of rocky reef in the new MPAs. Kelp restoration has the potential to play a valuable role as one of many integrated tools in an ecosystem-based management approach.

Key words: alternative stable state; ecosystem-based management; generalized linear modeling; giant kelp; *Macrocystis pyrifera*; marine protected area; marine reserve; Monte Carlo simulation; reproduction; southern California; *Strongylocentrotus franciscanus; Strongylocentrotus purpuratus.*

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Introduction

In taking an ecosystem-based approach to marine resource management, resource managers may need to account for interspecific interactions while trying to sustain harvests and conserve marine resources (Botsford et al. 1997, Halpern et al. 2010). Nearshore rocky reefs along the West Coast of North America may present ideal candidates for implementing and studying these types of management strategies (Rogers-Bennett 2007). In southern California, the herbivorous sea urchins *Strongylocentrotus purpuratus* (purple sea urchin) and/or *Strongylocentrotus franciscanus* (red sea urchin) can, in high densities, clear expanses of kelp forest resulting in urchin barrens, leaving the reef devoid of standing macroalgae (Dean et al. 1984, Harrold and Reed 1985, Steneck et al. 2002, Graham 2004). In this region, *Macrocystis pyrifera* (giant kelp) is the dominant biotic habitat forming component in kelp forests, supporting hundreds of species through trophic and/or structural associations (Graham 2004). Meanwhile, the *S. franciscanus* fishery, where urchins are harvested for their roe (i.e., both male and female gonads), is one of the most important commercial fisheries in California (Sonu 2003, Rogers-Bennett 2007). In 2010, *S. franciscanus* landings ranked 4th by weight (over 5,000 metric tons) and 5th in value (7.4 million US Dollars) (CDFG 2011). *S. purpuratus* however, are not targeted in these urchin fisheries. While a higher density of urchins in barrens might appear as a benefit to the fishery, the low availability of macroalgae for these herbivores can result in reduced urchin gonad production (Dean et al. 1984, Harrold and Reed 1985, Rogers-Bennett et al. 1995, Konar and Estes 2003), making *S. franciscanus* within barrens less valuable to the fishery (Kato and Schroeter 1985, Kalvass and Hendrix 1997, Sonu 2003). Therefore, ecosystem-based management strategies should prioritize the maintenance of both the harvested *S. franciscanus* populations and the biomass of their *M. pyrifera* food resources.

Even though urchin barrens can be relatively dynamic and short-lived elements of the kelp forest ecosystem (Harrold and Reed 1985, Graham 2004), globally they have been reported to persist for long periods on temperate reefs, in some cases for decades (Schiel 1990, Jackson 2001, Steneck et al. 2002, Shears and Babcock 2003, Smith et al. 2004, Norderhaug and Christie 2009). In some ecosystems, sea urchin consumption of kelp can be limited primarily by predation on urchins (Estes and Palmisano 1974, Dayton 1985, Edwards 2004). Since the southern sea otter was extirpated from southern California over 100 years ago (Tegner 1980, Estes and Duggins 1995), the primary remaining predators on urchins are *Panulirus interruptus* (California spiny lobster) and *Semicossyphus pulcher* (California sheephead) (Tegner and Dayton 1981, Cowen 1983, Tegner and Levin 1983, Lafferty 2004, Hamilton et al. 2011). Both of these species are heavily targeted by commercial and recreational fisheries in this region (Hamilton et al. 2007, CDFG 2010, CDFG 2011, Kay et al. 2012). In addition, thriving populations of abalone once served as competitors to urchins, but are currently ecologically extinct in much of the region (Tegner and Dayton 2000). Therefore, additional management actions may be necessary to increase urchin mortality in order to reduce the prevalence of barrens (Baskett and Salomon 2010).

While marine protected areas may ultimately play an important role in reducing the prevalence of urchin barrens by maintaining urchin predator populations (Shears and Babcock 2002, Shears and Babcock 2003, Guidetti 2006, Shears et al. 2012), it can take more than a decade for densities and/or size structures of their predators to increase beyond thresholds which result in reduced urchin populations and subsequent increases in macroalgal abundance (Guidetti and Sala 2007, Babcock et al. 2010, Salomon et al. 2010, Leleu et al. 2012). Further, crustose coralline algae can induce settlement of urchin larvae (Pearce and Scheibling 1990), potentially leading to recruitment facilitation in urchin barrens, resulting in barrens being maintained in an alternative stable state. Therefore, active restoration (i.e., "targeted sea urchin removals") may be necessary to initially return barrens to a macro-algal dominated kelp forest stable state (Baskett and Salomon 2010).

Kelp forests in Santa Monica Bay, California, adjacent to Los Angeles, the largest urban area on the west coast of the United States, are directly affected by anthropogenic impacts associated with urban development and human population increase. These include an extensive

and diverse set of stressors (e.g., sedimentation, urban runoff, pollution) in addition to both recreational and commercial fishing, that combine to contribute to the decline of productive, stable kelp habitat along this important stretch of coastline (Stull et al. 1987, Dojiri et al. 2003, Schiff 2003, Love 2006, Pondella 2009, Foster and Schiel 2010, Sikich and James 2010, Erisman et al. 2011). During the 1940s, *M. pyrifera* declined substantially near major sewage outfalls in the region (Wilson et al. 1977, Foster and Schiel 2010). Ultimately, outfalls were relocated further offshore and sewage received further processing. However, as the importance of *M. pyrifera* as a commercially harvested resource grew during this time period, overgrazing by urchins was implicated in its decline, leading to a variety of kelp restoration efforts during the 1950–70s. These involved kelp transplantation and herbivore control, primarily the killing of sea urchins (both *S. purpuratus* and *S. franciscanus*) by physical crushing or "chemical destruction" using quicklime. Additional efforts included removing herbivorous fishes via spearfishing and gillnets. Restoration efforts at multiple sites along Santa Monica Bay and Pt. Loma in San Diego County showed substantial recovery of kelp canopy. While some sites were subsequently impacted by winter storms, they appeared resilient and recovered in the 2–3 years following major storm events (Wilson et al. 1977). More recently (1990s, 2000s), relatively small scale pilot kelp forest habitat restoration projects in the Santa Monica Bay have demonstrated reestablishment of *M. pyrifera* after urchin removal at multiple 1–2 ha sites. During these restoration efforts, 98% of the urchins removed from the barrens were *S. purpuratus* (Ford and Meux 2010) suggesting that in this area *S. purpuratus* likely create or at least maintain these urchin barrens.

Larger scale kelp restoration is now planned along the Palos Verdes Peninsula at the southern end of Santa Monica Bay (Fig. 1). In addition, two MPAs (Point Vicente SMCA, Abalone Cove SMCA) were implemented in this area on 1 January 2012. Both of these "State Marine Conservation Areas" include the prohibition of commercial fishing for sea urchin within their boundaries. While MPAs in southern California can over time increase the *S. franciscanus* size structure and associated reproductive potential within their boundaries (Shears et al. 2012), they also represent an immediate loss of fishing habitat for the local commercial *S. franciscanus* fishery. Therefore, in this study we first evaluate the potential of kelp forest habitat restoration within the study area to increase the urchin gonad biomass available to the fishery, including only the gonad biomass from *S. franciscanus* above the legal minimum size limit. In particular, we compare the potential benefit of restoring all of the urchin barrens outside of the newly designated MPAs to the loss of fishing habitat within the MPAs, in terms of the overall gonad biomass available to the fishery. Next, using total gonad biomass as proxy for reproductive potential (Levitan 1991, Shears et al. 2012), we examine the degree to which restoration may increase the reproductive potential of *S. franciscanus*, including all mature urchins (i.e., those both above and below the legal minimum size limit) in estimates of total gonad biomass. In particular, we estimate the increase in *S. franciscanus* reproductive potential within the new MPAs if all barrens within their boundaries are restored.

In order to compare differences in gonad biomass amongst populations of urchins, it is necessary to incorporate urchin density, body size and size-specific gonad weight (Shears et al. 2012). Therefore, we address these two primary study objectives using Monte Carlo simulations (Haddon 2011) that synthesize urchin density and size structure data from a concurrent long term monitoring program with data empirically derived for this study. These data include estimates of the spatial extent of urchin barrens within the study area and habitat-specific relationships between urchin gonad size and body size. To establish parameters for these relationships to use in the simulations, *S. franciscanus* (and *S. purpuratus* for comparison) were collected from both kelp forest and urchin barren habitat, and the amount of gonad weight produced at a given body size (test diameter) was compared using generalized linear models.

Methods

Mapping and data from comprehensive monitoring surveys

The study area was bounded by the coastline extending from the commercial fishing boundary

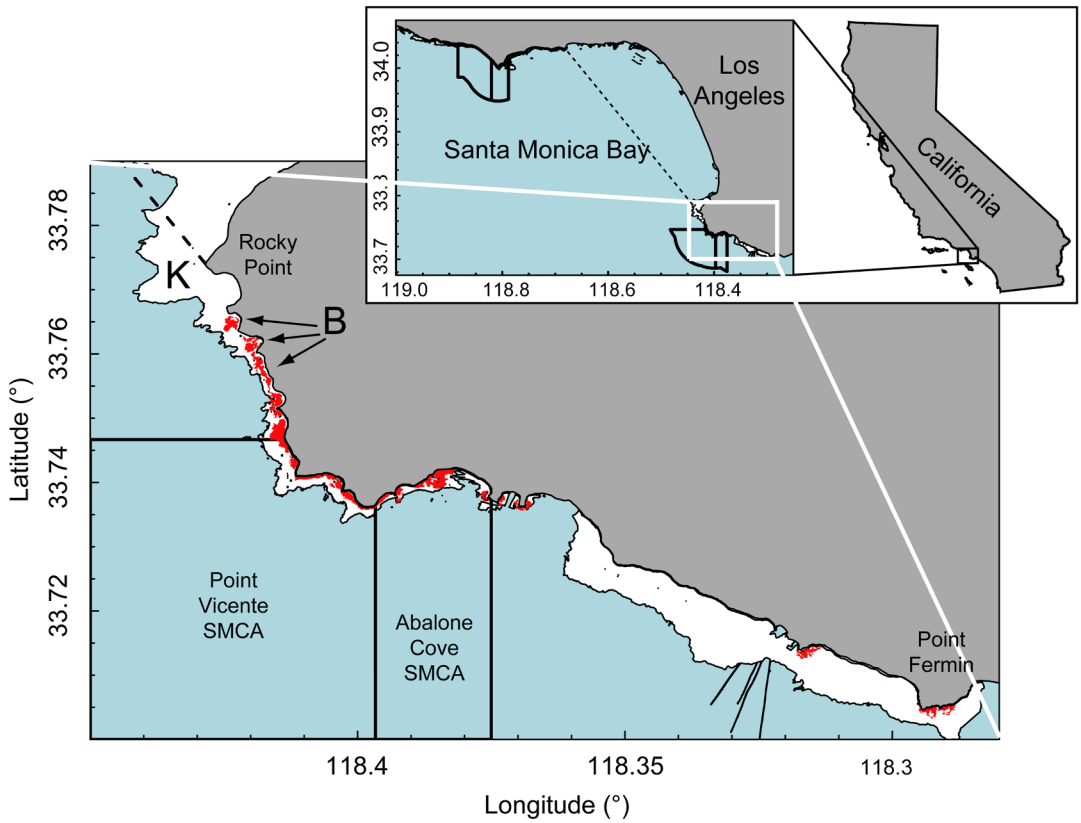

Fig. 1. Map of study area along the Palos Verdes Peninsula extending southeast from the commercial fishing boundary (dashed line) at Rocky Point, where some commercial fishing activities are prohibited inside Santa Monica Bay, to the nearshore rocky reef around Point Fermin. The extent of nearshore rocky reefs are shown in white (Claisse et al. 2012) and mapped urchin barrens are displayed in red. Urchins were collected for gonad analysis from 3 urchin barrens (B) and from haphazardly chosen sites within a large continuous kelp forest (K). The boundaries of the two adjacent MPAs in the study area (Point Vicente SMCA and Abalone Cove SMCA) are also shown.

(dotted line, Fig. 1) at Rocky Point southeast to Point Fermin (inclusive of the reef which surrounds this point), and seaward to the extent of nearshore rocky reefs as mapped in Claisse et al. (2012) (Fig. 1). Commercial urchin fishing was permitted at the time of data collection in the entire study area, with the closure within the two MPAs in the study area on 1 Jan 2012 having occurred after data collection had concluded.

We produced an estimate of the current (2011) spatial extent of urchin barrens in the study area to parameterize our simulations for this case study by combining information from a nearshore hard-bottom habitat map in Santa Monica Bay (Claisse et al. 2012), the two most recent sets of satellite imagery from Google Earth, and in-situ SCUBA surveys performed as part of an ongoing comprehensive monitoring program (protocols described brefily in following paragraph, and in more detail in Hamilton et al. 2010, Claisse et al. 2012). Urchin barren polygons were heads-up digitized only in areas where hard substrate was present (according to Claisse et al. 2012), but kelp canopy was not in the March 8th, 2011 satellite imagery. Further, GPS points (n = 301) from the in-situ SCUBA surveys (which provided information on densities of urchin and macroalgae cover) were used as training points to inform the heads-up digitizing process when mapping barren areas. The extent of urchin barrens were refined further using the November 15th, 2009 satellite imagery. The clarity and

calmness of the nearshore waters in this imagery permitted improved confirmation that the underlying substrate in nearshore areas mapped as barrens was suitable for macroalgae and thus had the potential to respond to habitat restoration. We used the PBSmapping package in R (R Development Core Team 2011) to plot the map figure shown here. Additionally, for use in the Monte Carlo simulations described below, functions in that package were used to measure the total area of urchin barrens, their areas inside and outside of MPAs in the study area, and the total area of nearshore hard bottom habitat (<30 m depth) within the two MPAs combined.

Strongylocentrotus franciscanus, *M. pyrifera* and understory macroalgae abundance per 60 m^2 band transect were extracted from data collected at sites in the study area from 2007 through 2011 following a standardized comprehensive community monitoring survey protocol; for more details on the protocol see (Hamilton et al. 2010, Claisse et al. 2012). Briefly, at each site, 30-m $\times$ 2-m transects were laid out in a depth stratified random design, with 2 benthic transects located in each of four depth zones: Inner (target depth 5 m; actual surveyed depths 3 to 7 m), Middle (target depth 10 m; actual surveyed depths 7 to 12 m), Outer (target depth 15 m; actual surveyed depths 10 to 18 m), and Deep (target depth 25 m; actual surveyed depths 18 to 30 m). Only depth zones containing rocky reef habitat at each site were sampled. Specific minimum size criteria were applied when counting macroalgal species (e.g., *M. pyrifera* taller than 1 m; *Eisenia arborea* taller than 30 cm). Abundance data in each depth zone at each site were averaged across transects and years, yielding a single replicate for each depth zone at each site to be used in the analyses. Also, abundance of macroalgae in 2011 was compared specifically between urchin collection sites (either urchin barren or kelp forest) for the gonad biomass analysis described below using a one-way ANOVA. When necessary, data were $\log_{10}(x + 1)$ transformed to meet model assumptions. *S. franciscanus* were also collected from each depth zone and their test diameter was measured to the nearest mm to quantify size frequency distribution. Mean test diameter amongst depth zones was compared with a one-way ANOVA followed by Tukey HSD tests for pairwise comparisons.

Because transects in the depth stratified random design from monitoring surveys did on occasion overlap patches of urchin barren and kelp forest habitat, additional surveys were completed in 2011 to parameterize the urchin barren *S. franciscanus* abundance per transect distributions for the Monte Carlo simulation models described below. Ten sites within the mapped urchin barren habitat were surveyed (2 transects per site) ensuring that each transect was haphazardly placed entirely within the barren. To parameterize the *S. franciscanus* abundance per transect distributions for the kelp forest habitat in the simulation model described below, 10 sites from the comprehensive long-term monitoring data in the study area were selected as kelp forest reference sites. These were sites with no urchin barrens observed on any transect. These urchin barren and kelp forest reference surveys were performed in the Inner depth zone to standardize them with the urchin collections made for gonad production analyses (see *Methods: Influence of habitat on gonad production*).

The influence of habitat (for urchin barren and kelp forest specific surveys) or depth zone (from comprehensive monitoring data) on *S. franciscanus* abundance per transect was investigated with model selection using the second-order bias corrected Akaike's Information Criterion (AICc) (Burnham and Anderson 2002). AICc includes an additional term to correct for bias related to small sample size (n) that becomes negligible when n is large (Akaike 1973, Anderson 2008). Akaike weights (w_i) were calculated to assess the relative likelihood of each model in a set and were interpreted as a weight of evidence in favor of the hypothesis represented by the model (Burnham and Anderson 2002). In each case two models were compared: model 1 estimated a habitat or depth zone specific mean abundance per transect and model 2 estimated a single mean abundance per transect for data from all habitats or depth zones pooled. Both assumed a negative binomial probability distribution with a log-link function. The "ecological" parameterization of the negative binomial was used following Bolker (2008). It is appropriate for positively skewed count data and is defined by a mean μ and an overdispersion parameter k that measures the amount of heterogeneity in the data (i.e., as k decreases the overdispersion increases). When k is large,

the variance approaches the mean and the negative binomial converges on a Poisson distribution (Zuur et al. 2009). Abundance per transect was rounded to nearest integer because negative binomial distribution requires discrete counts (Bolker 2008). Models were fitted and 95% likelihood profile confidence intervals were calculated using the glm.nb function in R (Venables and Ripley 2002, R Development Core Team 2011). Parameter estimates and confidence intervals were back transformed and converted to densities prior to plotting.

Influence of habitat on gonad production

A total of 690 *S. franciscanus* and 692 *S. purpuratus* were collected over four sampling dates in 2011 (1 April, 22 April, 12 May, and 26 May) from urchin barren and kelp forest habitat (~4 m depth) within the study area (Fig. 1). Given the observed spatial and temporal variability in urchin population characteristics, it was important they be obtained locally to properly evaluate urchin gonad production (Bennett and Giese 1955, Kato and Schroeter 1985, Lester et al. 2007, Ebert et al. 2011, Shears et al. 2012). On each sampling date, typically 30 *S. franciscanus* and 30 *S. purpuratus* were collected from 3 haphazardly selected sites within a large expanse of kelp forest habitat (K, Fig. 1) and from each of three urchin barrens sites (B, Fig. 1)—an exception being that on the first sampling date only two kelp forest sites were sampled. To minimize the potential for edge effects to impact gonadal production (Dean et al. 1984), urchins were collected from more than 20 m from the edge of a kelp/barren transition in all cases. At each site, the first 30 urchins encountered that could be removed without damage were collected. Urchins were then transported to the lab in coolers, where test diameter was measured to the nearest mm and gonads were removed and weighed to the nearest 0.01 g. For each species, mean test diameter was compared between habitat types using a one-way ANOVA.

The relationship between urchin test diameter and gonad weight was modeled using an allometry model with an adjustment for the size when gonads begin to develop following Ebert et al. (2011):

$$G = \alpha(L - R)^{\beta} \qquad (1)$$

where G is gonad weight (g), L is urchin test diameter (mm), R is the minimum test diameter when gonads begin to develop and α and β are 2 fitting parameters which have no direct biological meaning. For *S. franciscanus*, R was 40 mm (Tegner and Dayton 1981, Kato and Schroeter 1985), and for *S. purpuratus*, R was 16 mm (Kenner and Lares 1991). Accordingly, urchins below diameter R were excluded from the remaining analysis. These sizes represent the minimum size each urchin species has been observed producing viable gametes in the Southern California Bight, which is generally smaller than that of urchins collected in more northern areas of the Pacific coast (Kato and Schroeter 1985, Kenner and Lares 1991). For both species, observations from the present study were consistent with these sizes.

The gonad weight at length (Eq. 1) was fitted by minimizing the negative log-likelihood using the mle2 package in R (R Development Core Team 2011), assuming that G follows a lognormal distribution with mean determined by Eq. 1 and the standard deviation of the logarithm (sdlog). A lognormal distribution is typical for a distribution of sizes of individuals that grow exponentially (Bolker 2008). These assumptions were confirmed by visually comparing the predicted lognormal distribution density with the sample density of gonad weights for a given test size range (Bolker 2008).

The influence of collection date and habitat type on the relationship between gonad weight and urchin test diameter using the previously described model (Eq. 1) were investigated via model selection using AICc as previously described (Burnham and Anderson 2002). For each species, four models were included in a model set: (Habitat) unique parameters (α, β, sdlog) are estimated for urchins collected in each habitat type (urchin barren or kelp forest); (Date) unique parameters (α, β, sdlog) are estimated for each collection date; (Habitat $\times$ Date) unique parameters (α, β, sdlog) are estimated for each habitat type on each collection date; (Null Model) identical parameters (α, β, sdlog) are estimated for both habitat types across all collection dates.

Due to differences in the size distributions of urchins collected in kelp forest and barren habitats (see *Results: Influence of habitat on gonad production*), we used a bootstrapping approach to

directly compare differences in gonad weight at a specific test diameter for each species. A size was selected where there was substantial overlap in the test diameter size structures of urchins collected in each habitat and thus would provide the most reliable estimates for comparison. Bootstrapping was used to estimate 95% confidence intervals (Haddon 2011) around the mean gonad size predicted by the models at 84 mm for *S. franciscanus* and 45 mm for *S. purpuratus*. 84 mm was also selected because it has important applied value for *S. franciscanus* as the size just above the commercial minimum size limit. Bootstrapping involved random re-sampling with replacement from the original data set to generate an equivalent data set, re-estimating model parameters for the highest ranked model from the new data set and then substituting the new parameter estimates back into Eq. 1 to estimate mean gonad weight at the given urchin test diameter. This was repeated 1000 times and the gonad weight estimates at 2.5% and 97.5% of these new distributions were taken as the lower and upper 95% confidence limits.

Potential of kelp restoration

The empirical data were synthesized to address our two primary study objectives using Monte Carlo simulations (Haddon 2011). The first objective was to evaluate the potential of kelp forest habitat restoration within the study area to increase the urchin gonad biomass available to the fishery (i.e., gonad biomass only in urchins above the legal minimum size limit). Monte Carlo simulations permitted us to incorporate the variability associated with the estimated population parameters for *S. franciscanus* density, size structure and size-specific gonad biomass while estimating the gonad biomass (and 95% confidence intervals) of *S. franciscanus* above the legal size limit ($\geq$84 mm test diameter), assuming conditions on our sampling occasion with the highest size-specific gonad biomass. More specifically we predicted the potential of restoring all of the urchin barrens in the study area outside of the newly designed MPAs to offset the loss of fishing habitat within the MPAs in terms of changes in the gonad biomass available to the fishery. The gonad biomass available to the fishery was therefore estimated and compared among 3 scenarios: (1, "Barren") in all mapped urchin barrens in our study area outside of MPAs, (2, "Restored Barren") in the urchin barrens outside of MPAs assuming they were restored to kelp forest conditions and (3, "MPAs") the entire rocky reef habitat area within the new MPAs based on the recently sampled conditions prior to MPA establishment. For each scenario, 1000 simulation trials were run, with the mean of the trials being the final estimate of the overall gonad biomass, and the estimates at 2.5% and 97.5% of the distribution of all trials taken as the lower and upper 95% confidence limits (Haddon 2011).

For the Monte Carlo simulations, each trial was started by estimating the total abundance of *S. franciscanus* for the given scenario. Total abundance was the sum of urchin abundances per 60 m^2 transect, randomly drawn (using the R function "rnbinom") from a negative binomial distribution until the sum of their transect areas equaled the total area of the habitat within the scenario. In all trials, the negative binomial parameters μ and k (Bolker 2008) were also randomly drawn (using the R function "rnorm") from their own Gaussian distributions according to the parameter estimates and their associated standard errors obtained from fitting a negative binomial distribution to the available empirical abundance per transect data described previously in the various habitats and depth zones.

Then for each urchin in the trial, a test diameter was randomly drawn (using the R function "rnorm") from the Gaussian distribution fitted to the empirical size structure data for the appropriate habitat or depth zone in each scenario. If the urchin was $\geq$84 mm test diameter (i.e., just above the legal minimum size limit in southern California), its gonad weight (G) at length was randomly drawn (using the R function "rlnorm") from the log normal distribution following Eq. 1, using the α, β and sdlog parameters from the maximum reproductive period for the appropriate habitat (either Barren or Kelp). The sum of all gonad weights from legal sized urchin in each trial was the overall gonad biomass estimate for that trial.

For the MPA scenario, we estimated depth-zone specific population parameters due to differences in *S. franciscanus* abundance per transect and size structure in the empirical data (see *Results: Mapping and comprehensive monitor-*

ing surveys). Additionally, rocky reef habitat area within the MPAs (Fig. 1) was assumed to be equally divided amongst the 4 depth zones (Claisse et al. 2012). Further, because urchin barrens were found almost exclusively in the Inner and Middle depth-zones, the urchin barren habitat area within the MPAs (Fig. 1) was assumed to be divided equally amongst the Inner and Middle depth zones. Therefore, for each MPA trial, gonad biomass was first estimated separately for the habitat area within each of the 4 depth zones in the MPAs and then summed to yield the overall gonad biomass within the MPAs.

The second primary study objective was to evaluate the potential for kelp forest habitat restoration to increase the total reproductive potential of *S. franciscanus*, using total gonad biomass as proxy (Levitan 1991, Shears et al. 2012). Therefore, we ran the same three Monte Carlo simulation scenarios described previously, but did not exclude the mature urchins that were below the legal minimum size limit (84 mm) from contributing to the total gonad biomass estimates for each trial. Additionally, to examine the potential for restoration to increase the total reproductive potential of all *S. franciscanus* within the MPAs, we ran a fourth simulation scenario, where all urchin barren habitat within the MPAs was assumed restored to kelp forest habitat. As before, a mean and 95% confidence intervals were calculated from 1000 simulation trials for each scenario.

Results

Mapping and comprehensive monitoring surveys

The mapped extent of urchin barrens in the study area (Fig. 1) has a total area of 61 ha, 36 ha of which are on nearshore rocky reefs that lie outside of the MPAs in the area. Nearshore rocky reef habitat (<30 m depth) inside the two MPAs has a total area of 109 ha, 25 ha of which was mapped as urchin barren.

Transects in urchin barrens had 5.2 times more *S. franciscanus* and 11.7 times more *S. purpuratus* than those exclusively in kelp forest habitat (Fig. 2, Table 1). The depth range for these transects were 3–7 m and these included the urchin collection sites for gonad analysis. Therefore, habitat type exhibited a clear effect on abundance per transect of *S. franciscanus* and *S. purpuratus* based on AIC differences and 95% confidence intervals (Table 2c, d, Fig. 2). The models that estimated habitat specific means had substantially lower AICc values (differences of 7.7 and 27, respectively) and received very high levels of the support (98% and 100% according to w_i, respectively) relative to the single mean models. Note an AICc difference greater than 2 can be considered equivalent to a significant difference (Burnham and Anderson 2002). Also, *S. purpuratus* were over 10 times more abundant than *S. franciscanus* in urchin barren habitat (Fig. 2).

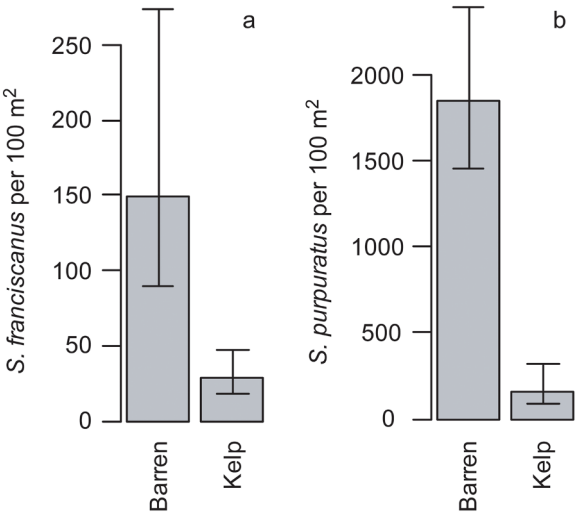

Fig. 2. Habitat specific density patterns of (a) *Strongylocentrotus franciscanus* and (b) *S. purpuratus* from surveys with transects entirely in urchin barren or kelp forest habitat. Error bars are 95% likelihood profile confidence intervals assuming a negative binomial probability distribution.

Using data from the depth stratified random sampling comprehensive monitoring program (Claisse et al. 2012) in the study area, depth zone exhibited a clear effect on abundance per transect of *S. franciscanus* based on AIC differences and 95% confidence intervals (Table 2e, Fig. 3). The model that estimated depth zone specific means had a substantially lower AICc value (difference of 17) and received all the support according to w_i relative to the single mean model. Transects in Inner and Middle depth zones (transect depth range 3–7 m and 7–12 m, respectively) had more than double the *S. franciscanus* density of the Outer depth zone (transect depth range 10–18 m),

Table 1. *Strongylocentrotus franciscanus* population characteristics from urchin barren habitat (Barren), kelp forest habitat (Kelp) or depth zone (Inner, Middle, Outer, Deep) specific collections.

Characteristic	Barren	Kelp	Inner	Middle	Outer	Deep
Abundance/transect						
n (sites)	10	10	21	23	15	7
μ	4.49	2.84	3.77	3.71	2.78	1.80
μ SE	0.28	0.24	0.20	0.13	0.28	0.52
k	1.27	1.96	1.28	2.56	0.89	0.57
k SE	0.52	0.95	0.38	0.77	0.33	0.37
Test diameter (mm)						
n (individuals)	360	330	417	649	452	115
μ	61	92	76	72	73	95
SD	15	11	22	24	30	24
Tukey HSD			A	A	A	B

Notes: Sample sizes (*n*) and parameter estimates for the negative-binomial model of mean abundance per transect and for the Gaussian model of mean test diameter (mm). See *Methods* for descriptions of individual parameters. Tukey HSD: differences between letters represent a significant pairwise comparison, alpha = 0.05.

and around 7 times the density of the Deep depth zone (transect depth range 18–30 m) (Table 1). Additionally, the mean test diameter of urchins collected during comprehensive monitoring were significantly different among depth zones ($F_{3,\,1629} = 27.1$, $P < 0.001$). Mean test diameter was around 20 mm greater in the Deep depth zone, than those in the Inner, Middle and Outer depth zones, with no other significant differences among depth zones (Tukey HSD, Table 1).

Influence of habitat on gonad production

The urchin barren habitat at the Palos Verdes Peninsula from which urchins were collected was almost completely devoid of *M. pyrifera* (0.01 ± 0.1 per m^2; mean ± SE) and understory macroalgae (0.05 ± 0.4 per m^2). This was significantly different from the kelp forest habitat from which urchins were collected (*M. pyrifera*: 1.6 ± 0.6 per m^2; ANOVA, $\log_{10}(x+1)$ transformed, $F_{1,4} = 91.0$, $P < 0.001$) and understory macroalgae (1.8 ± 0.9 per m^2; ANOVA, $\log_{10}(x+1)$ transformed, $F_{1,4} = 14.6$, $P = 0.02$). Urchins collected for gonad analysis in kelp forest habitat tended to be larger than those collected in urchin barrens (Fig. 4). Mean test diameter of *S. franciscanus* from kelp forest habitat (92 ± 0.7 mm) was significantly larger than those in urchin barrens (61 ± 0.7 mm; [$F_{1,\,688} = 902$, $P < 0.001$]). Mean test diameter of *S. purpuratus* from kelp forest habitat (55 ± 0.4 mm) was also significantly larger than those in urchin barrens (36 ± 0.4 mm; [$F_{1,\,690} = 1121$, $P < 0.001$])

Table 2. Model selection results, ranked according to the difference in AICc (ΔAICc) and Akaike Weight (w_i). Np.: number of estimated parameters in each model. (a, b) Models representing the influence of habitat type (Habitat: kelp forest or urchin barren), and/or collection date (Date) on the relationship between mean gonad weight and urchin test diameter for either *Strongylocentrotus franciscanus* or *S. purpuratus*. (c, d) Models representing the influence of habitat type (Habitat: kelp forest or urchin barren) on either *S. franciscanus* or *S. purpuratus* abundance per transect. (e) Models representing the influence of depth (Depth zone: Inner, Middle, Outer, Deep) on *S. franciscanus* abundance per transect.

Model	ΔAICc	AICc	w_i	Np.
a) Gonad, *S. franciscanus*				
Habitat × Date	0	3763	1.0	24
Habitat	159	3922	0.0	6
Date	696	4459	0.0	12
Null model	726	4489	0.0	3
b) Gonad, *S. purpuratus*				
Habitat × Date	0	1460	1.0	24
Habitat	115	1575	0.0	6
Date	190	1650	0.0	12
Null model	230	1690	0.0	3
c) Abundance/transect, *S. franciscanus*				
Habitat	0.0	196.0	0.98	4
Single mean	7.7	203.7	0.02	2
d) Abundance/transect, *S. purpuratus*				
Habitat	0	271	1.0	4
Single mean	27	298	0.0	2
e) Abundance/transect, *S. franciscanus*				
Depth zone	0	580	1.0	8
Single mean	17	597	0.0	2

Urchins of both species collected in kelp forest habitat tended to have higher gonad weight at length than those collected in urchin barren habitat (Fig. 5 and 6; Tables 3 and 4). For each species, model selection provided strong support for the model that included the influence of both habitat type and collection date (Habitat × Date, Table 2 a, b). These models received 100% of total w_i due to the very large AICc differences with the other models in each set (i.e., ≥115). For *S. franciscanus*, mean gonad weight at 84 mm (as predicted by the model) collected in kelp forest habitat was highest on the 26 May 2011 collection (Fig. 7; Table 3), 484% greater than the mean gonad weight of urchins collected in urchin barren habitat on that date. The greatest difference (659% higher in kelp habitat) was observed on 12 May 2011, due to a particularly low mean

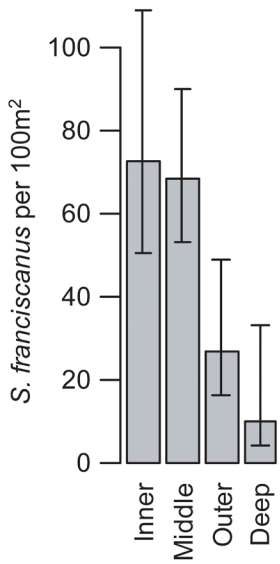

Fig. 3. Depth zone specific density patterns of *Strongylocentrotus franciscanus*. Error bars are 95% likelihood profile confidence intervals assuming a negative binomial probability distribution.

gonad weight in the barrens (Fig. 7; Table 3). A similar pattern was also observed in *S. purpuratus*; mean gonad weight (as predicted by the model) at 45 mm collected in kelp forest habitat was highest on 12 May 2011 (Fig. 7; Table 3), 333% greater than the mean gonad weight of urchins collected in urchin barren habitat.

Potential of kelp restoration

Strongylocentrotus franciscanus density and size structure were synthesized with the gonad production model via Monte Carlo simulations (assuming conditions on our sampling occasion with the highest size-specific gonad biomass) to address our two primary study objectives. The first objective was to evaluate the potential of kelp forest habitat restoration to increase the urchin gonad biomass available to the fishery within the study area. Therefore, these simulations only included the gonad biomass from *S. franciscanus* above the legal minimum size limit. Under these conditions, urchin barrens restored to kelp forest habitat would potentially have 864% greater *S. franciscanus* gonad biomass available to the fishery per unit area (Barren: 1.1 g/m^2, 95% CI 0.6–1.8 g/m^2 ; Restored Barren: 10.6 g/m^2, 95% CI 6.5–16.4 g/m^2). Therefore, if all 36 ha of urchin barren mapped outside of the MPAs in the study area were restored to kelp forest, we would expect a net increase of 3435 kg of *S. franciscanus* gonad biomass available to the fishery (i.e., Restored Barren gonad biomass − Barren gonad biomass: Fig. 8). This represents an offset of 52% of the gonad biomass that used to be available to the fishery (6663 kg) and is now protected within the 109 ha of rocky reef habitat within the two new MPAs.

The second objective was to evaluate the potential of kelp forest habitat restoration to increase the overall reproductive potential of *S. franciscanus* populations. Therefore, our second set of simulations included all mature *S. franciscanus* in estimates of total gonad biomass (i.e., those both above and below the legal minimum

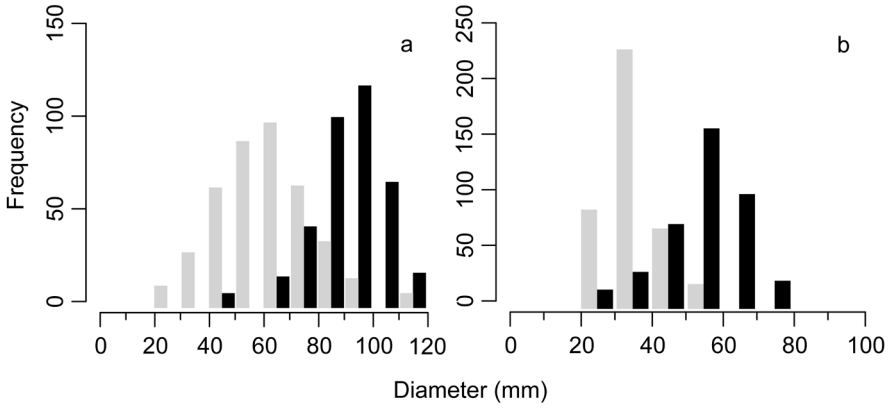

Fig. 4. Urchin test diameter frequency (10 mm size classes) of (a) *Strongylocentrotus franciscanus* and (b) *S. purpuratus* collected from urchin barren (gray) or kelp forest habitat (black).

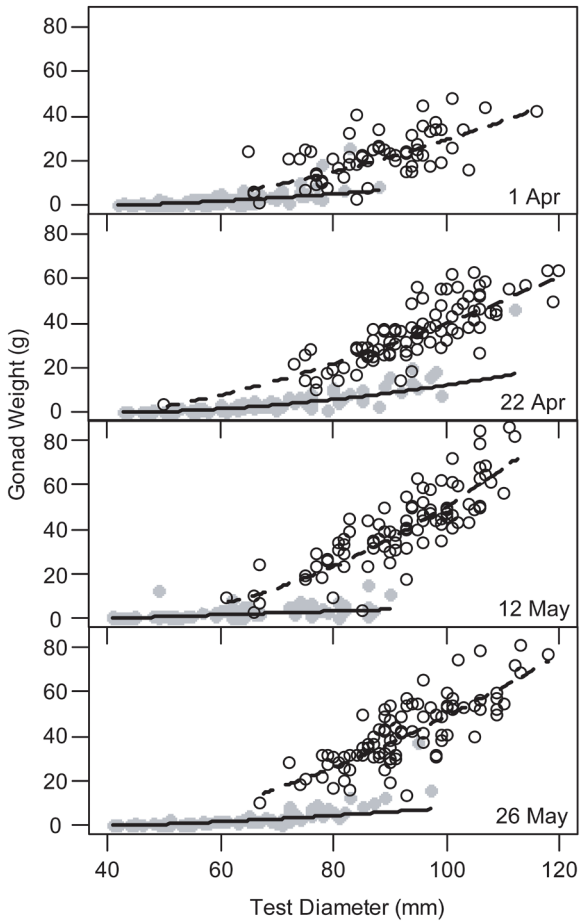

Fig. 5. *Strongylocentrotus franciscanus* relationship between mean gonad weight (g) and urchin test diameter (mm) based on the habitat (Barren: grey circles and solid lines; Kelp: open circles and dashed lines) and collection date specific model which received the most support (Habitat × Date, Table 2). Parameter estimates from which the curves are plotted are reported in Table 4.

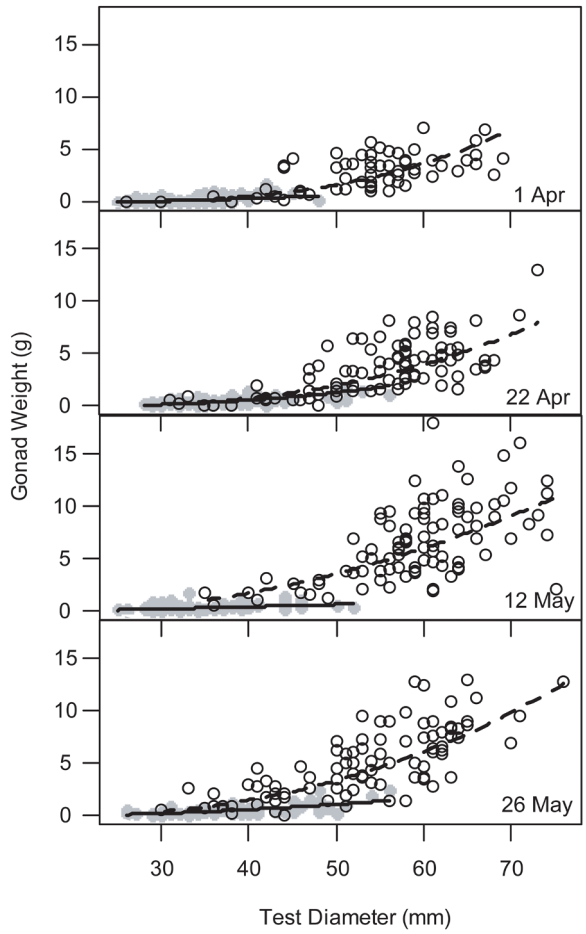

Fig. 6. *Strongylocentrotus purpuratus* relationship between mean gonad weight (g) and urchin test diameter (mm) based on the habitat (Barren: grey circles and solid lines; Kelp: open circles and dashed lines) and collection date specific model which received the most support (Habitat × Date, Table 2). Parameter estimates from which the curves are plotted are reported in Table 4.

size limit) to examine differences in reproductive potential pre- and post-restoration. Under these conditions, restored barrens would have 132% greater *S. franciscanus* total gonad biomass per unit area restored (Barren: 5.2 g/m^2, 95% CI 2.9–8.7 g/m^2; Restored Barren: 12.1 g/m^2, 95% CI 7.6–18.9 g/m^2). If the 23% of the rocky reef habitat area within the two new MPAs (25 of 109 ha) estimated to be urchin barren were restored (while all other urchin populations parameters remained the same), we would expect a 15% increase in total *S. franciscanus* reproductive potential within the new MPAs (gonad biomass within MPAs with existing barrens: 9.7 g/m^2, 95% CI 7.6–12.3 g/m^2; gonad biomass within MPAs with barrens restored: 11.2 g/m^2, 95% CI 8.9–14.2 g/m^2).

Discussion

Kelp forest habitat restoration through targeted sea urchin removals can potentially result in nine times more *S. franciscanus* gonad biomass

Table 3. Summary of urchin gonad weight at length (test diameter) parameter estimates and descriptive statistics for *Strongylocentrotus franciscanus* and *S. purpuratus* collected in urchin barren habitat (Barren) and kelp forest habitat (Kelp).

Date	Weight (g) at length†		%	*n*‡		Diameter (mm)§	
	Barren	Kelp		Barren	Kelp	Barren	Kelp
S. franciscanus, 84 mm length							
01 Apr 11	5.9 (4.6–8.3)	17.7 (15.1–20.1)	200	89	60	61 (42–88)	88 (65–116)
22 Apr 11	7.0 (5.7–7.9)	25.2 (23.1–26.7)	260	86	90	69 (43–112)	94 (50–120)
12 May 11	3.7 (2.6–5.3)	28.1 (25.5–31.6)	659	78	90	62 (41–90)	92 (61–112)
26 May 11	5.2 (3.8–7.0)	30.4 (28.4–32.6)	484	79	90	63 (41–97)	93 (67–118)
All data	5.2 (4.5–6.4)	25.2 (23.7–26.8)	385	332	330	64 (41–112)	92 (50–120)
S. purpuratus, 45 mm length							
01 Apr 11	0.5 (0.4–1.1)	1.0 (0.7–1.5)	100	90	62	33 (25–48)	53 (26–69)
22 Apr 11	0.7 (0.5–0.9)	1.2 (1.0–1.8)	71	90	90	37 (28–56)	54 (31–73)
12 May 11	0.6 (0.5–1.0)	2.6 (1.8–3.3)	333	90	90	34 (25–52)	59 (35–75)
26 May 11	0.9 (0.6–1.0)	2.4 (1.9–3.0)	167	90	90	38 (26–56)	53 (30–76)
All data	0.7 (0.6–0.9)	1.6 (1.4–2.0)	129	360	332	35 (25–56)	55 (26–76)

† Values are means with 95% CI in parentheses.
‡ Sample size (*n*) after *S. franciscanus* <40 mm diameter (minimum size at reproduction) were excluded from sample for analysis.
§ Values are means with ranges in parentheses.

available to the local commercial fishery (i.e., only including urchin over the legal minimum size limit) per unit area of urchin barren restored to kelp forest, with more modest increases also expected in terms of reproductive potential. Even though *S. franciscanus* were over five times more abundant in urchin barrens than in kelp forest reference sites, this was offset by their lower mean test diameter and very low size-specific gonad production. The population characteristics we observed for *S. franciscanus* and *S. purpuratus* in urchin barrens were typical of those observed in barrens elsewhere along the western Pacific coast of North America (Pearse et al. 1970, Dean et al. 1984, Harrold and Reed 1985, Konar and Estes 2003). When all mature urchins were included in the total gonad biomass estimates from our simulations to examine reproductive potential, results suggest restoring barren habitat could more than double the per unit area reproductive potential of *S. franciscanus* within urchin barrens. However, Shears et al. (2012) found that *S. franciscanus* reproductive potential was seven times greater in a small marine reserve studied in the northern Channel Islands in California compared to populations from unprotected comparison sites. This was mostly attributed to the larger size of urchins in this population that had not been fished since the reserve was created in 1978. Differences between

Table 4. Urchin gonad weight at length (test diameter) parameter estimates *Strongylocentrotus franciscanus* and *S. purpuratus* collected in urchin barren habitat (Barren) and kelp forest habitat (Kelp).

Date	Barren			Kelp		
	α	β	sdlog	α	β	sdlog
S. franciscanus						
01 Apr 11	0.0360	1.35	0.78	0.0360	1.64	0.53
22 Apr 11	0.0068	1.83	0.79	0.0900	1.49	0.24
12 May 11	0.1000	0.94	1.13	0.0230	1.88	0.37
26 May 11	0.0300	1.36	0.91	0.0860	1.55	0.25
All data	0.0390	1.29	0.94	0.0340	1.75	0.40
S. purpuratus						
01 Apr 11	0.0015	1.73	1.12	0.00003	3.06	0.68
22 Apr 11	0.0003	2.40	0.66	0.0001	2.70	0.65
12 May 11	0.0134	1.11	0.64	0.0030	2.01	0.47
26 May 11	0.0031	1.67	0.63	0.0010	2.31	0.60
All data	0.0029	1.62	0.81	0.0002	2.68	0.67

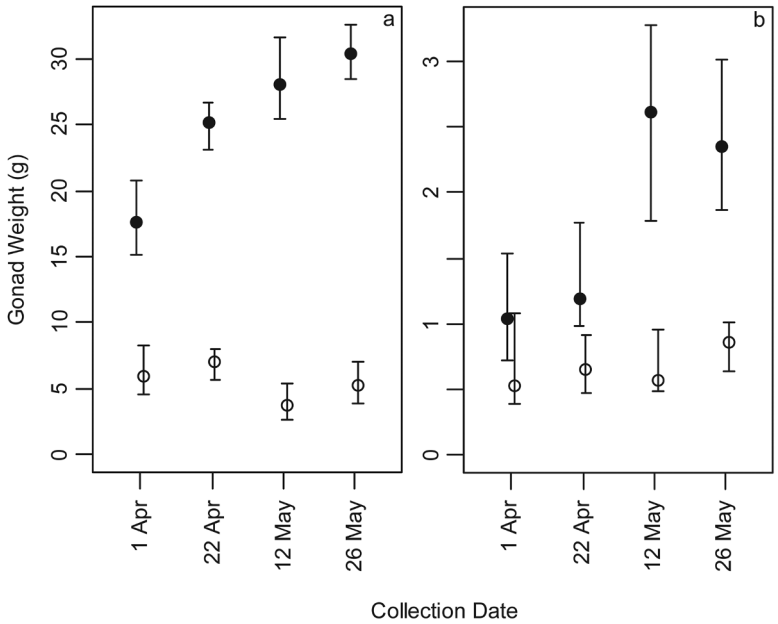

Fig. 7. Mean gonad weight (g) at 84 mm test diameter for (a) *Strongylocentrotus franciscanus* and at 45 mm test diameter for (b) *S. purpuratus* in urchin barren (open circle) and kelp forest (black filled circle) habitat. Error bars are 95% bootstrap confidence intervals based on the models which received the most support (Habitat × Date, Table 2).

gonad weight at length among sites or habitats were not investigated in that study; a single gonad weight at length model was used for all of their calculations. Our simulations of the reproductive potential within the new MPAs, with and without the barrens restored, produced estimates of total gonad biomass per m^2 (i.e., reproductive potential) that were similar to estimates from the unprotected sites examined in Shears et al. (2012). This is what we would expect since our data were collected before the MPAs were established in our study area. Therefore, for fished *S. franciscanus* populations, kelp restoration may present a management tool for increasing the gonad biomass available to a local fishery. While over the longer term (i.e., decades), MPAs which prohibit urchin fishing appear to possess greater potential to increase the reproductive potential of *S. franciscanus* populations, by building up and maintaining the abundance of larger individuals with high individual reproductive potentials.

A major assumption associated with our approach was that restoration would result in *S. franciscanus* populations with similar characteristics as those in the kelp forest reference sites. Previous efforts to remove urchins from barrens have demonstrated the re-establishment of macroalgal communities, typically within a year (Wilson et al. 1977, Andrew and Choat 1982, Shears and Babcock 2002, Ford and Meux 2010). Since urchin gonads are used for energy storage in addition to reproduction, gonad production is strongly related to the amount of macroalgal food resources available at very local scales (meters) (Bernard 1977, Dean et al. 1984, Harrold and Reed 1985, Kato and Schroeter 1985, Rogers-Bennett et al. 1995). Therefore, once kelp is reestablished, normal reproductive activity would be expected. However, these and other population characteristics of urchins in re-established kelp forests (i.e., density, size structure, and gonad weight at length relationship) have not been thoroughly empirically examined post-restoration. Further research is needed to determine the rate and degree to which these characteristics respond to restoration. Additionally, pre- and post-restoration monitoring should take a comprehensive approach (Hamilton et al. 2010, Shears et al. 2012), including measurements

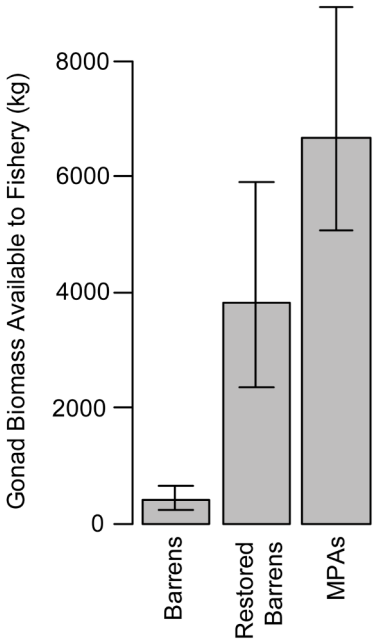

Fig. 8. The overall *Strongylocentrotus franciscanus* gonad biomass (kg) available to the fishery (i.e., only from urchins above the legal minimum size limit) and 95% confidence intervals estimated from Monte Carlo simulations under 3 scenarios: (Barrens) in all mapped urchin barren habitat outside of MPAs in the study area, (Restored Barrens) in all mapped urchin barren habitat outside of MPAs in the study area if it was restored to kelp forest, and (MPAs) in the rocky reef habitat now protected within the two MPAs in the study area.

of density and size structure of relevant fishes and invertebrates, plus appropriate measures of the algal community, so that other interspecific interactions can also be accounted for.

Based upon the Monte Carlo simulations, restoration of all 36 ha of urchin barren habitat mapped in the study area outside of the two new MPAs would offset more than half of the *S. franciscanus* gonad biomass which is now unavailable to the fishery due to the establishment of these MPAs. This result however, may also be somewhat conservative, because we may have overestimated the amount of gonad biomass now protected within the MPAs. The model we used to estimate gonad biomass in kelp forest habitat within the MPAs was based on our collections of urchins at relatively shallow (~4 m) depths. However, *S. franciscanus* collected at deeper depths (>14 m) can exhibit significantly smaller gonads than those at more shallow sites (Rogers-Bennett et al. 1995). Therefore, restoration may have the potential to offset an even greater proportion of what is no longer available to the fishery within the study area. While the Palos Verdes Peninsula is a primary *S. franciscanus* commercial harvesting ground, close to many of the major fishing ports in Los Angeles County (Kato and Schroeter 1985), we should point out that given the spatial scale of our case study, we do not address what the losses in fishing grounds within these two new MPAs and what the fishery benefits from restoration represent within the context of *S. franciscanus* landings across southern California. Additional analysis, incorporating other spatial fisheries information, would be needed to do so.

Our approach estimated differences between habitat conditions (i.e., urchin barren and kelp forest) assuming the size-specific distribution of *S. franciscanus* gonad biomass at its highest level during our sampling. Since the gonad biomass of urchins we collected in barrens remained low throughout our sampling period, and appears to remain low throughout the year (Harrold and Reed 1985), a net benefit from restoration, in terms of gonad biomass available to the fishery and reproductive potential, would be generally expected across all seasons. However, the magnitude of that benefit will be temporally dependent. Within kelp forests, the size-specific urchin gonad biomass increased substantially over the course of our sampling period. *S. franciscanus* gonad production and spawning seasonality can have high spatial and temporal variability along the West Coast of North America, with spawning potentially occurring somewhere in the region throughout the year (Bennett and Giese 1955, Bernard 1977, Kato and Schroeter 1985) and likely even varying across sites in southern California during a single season (Pearse et al. 1970). However, a clear pattern can be observed in *S. franciscanus* harvested for the commercial fishery in the northern Channel Islands in southern California, exhibiting peak gonad size around late October/early November, and minima in late April/early May (S. Teck, *unpublished data*). A similar pattern was also observed in the seasonality of urchin roe yield (i.e., gonad weight as a percentage of total body weight) at a

commercial processing plant in southern California (Kato and Schroeter 1985). If *S. franciscanus* in our study area followed this pattern, it would again suggest that our results may be conservative, with even greater benefits of restoration being expected if sampling had occurred during a peak gonad biomass period in the fall. Nevertheless, with respect to the applicability of our study to other areas in the State, the mean gonad size of *S. franciscanus* at 84 mm test diameter collected on 3 of our sampling events (Table 3, 4) were very similar to those landed in the commercial fishery at Fort Bragg, in northern California (35 g; Kalvass and Hendrix 1997) and Santa Barbara, in southern California (27 g; S. Teck, *unpublished data*). These gonad sizes from the harvested urchins come from samples averaged across seasons over multiple years (1986–1989 and 2008–2011, respectively), suggesting that the gonad weights used in our simulation models are typical of what is collected in the fishery across California.

Spatial and annual variability in the magnitude of benefit from kelp restoration will also depend on both stochastic and more regular patterns of environmental factors that influence kelp production. Relatively infrequent large scale storm events and ENSO related warm water events can substantially reduce kelp abundance across large regions. However, kelp can recover rapidly once normal conditions resume (Kato and Schroeter 1985, Tegner and Dayton 1991, Steneck et al. 2002, Edwards 2004, Edwards and Estes 2006, Parnell et al. 2010, Cavanaugh et al. 2011) and the resilience of kelp forests would likely benefit from restoration prior to such events (Wilson et al. 1977). In some areas, where there are consistently high waves associated with annual winter storms, this regular wave disturbance may have a greater impact on kelp production than urchin grazing intensity (Cavanaugh et al. 2011, Reed et al. 2011). For these areas, the expected benefits of kelp restoration would be more limited.

In a recent pilot kelp restoration project in Santa Monica Bay, which was successful in reestablishing giant kelp to densities above nearby kelp forest reference sites, 98% of the urchins removed from the barrens were *S. purpuratus* (Ford and Meux 2010). Given that *S. purpuratus* were about 12 times denser than *S. franciscanus* in barrens in our study area, we suggest that future restoration efforts in this region should remove only *S. purpuratus* from barrens. This would likely still result in reestablishment of *M. pyrifera*, while leaving the remaining *S. franciscanus* to benefit the fishery once gonad production resumes at normal levels. Recovery of seasonal gonad production can occur rapidly once sufficient food sources become available (Harrold and Reed 1985, Tegner 1989). Further, normal gonad production in *S. franciscanus* at densities higher than were observed in barrens in our study area can be supported under non-barren conditions (Harrold and Reed 1985, Rogers-Bennett et al. 1995).

This study provides an additional metric with which to evaluate the potential of kelp restoration projects, incorporating multiple population characteristics into an overall model of urchin gonad biomass available to a fishery and urchin reproductive potential. Given the importance of urchin fisheries throughout California and elsewhere globally (Kato and Schroeter 1985, Kalvass and Hendrix 1997, Sonu 2003, Rogers-Bennett 2007), and the impact and potentially increasing prevalence of urchin barrens (Dean et al. 1984, Harrold and Reed 1985, Steneck et al. 2002, Konar and Estes 2003, Graham 2004), kelp restoration by removing urchins from barrens may become a management strategy considered more often at the local level. The Palos Verdes Peninsula provides an important case study for implementing MPAs and kelp restoration within a single managed area adjacent to the largest urban area along the West Coast of North America. Building and maintaining higher densities and larger size structures of adult *S. franciscanus* within MPAs will serve to reduce potential Allee effects on fertilization success (Levitan et al. 1992, Quinn et al. 1993, Lundquist and Botsford 2004, Lundquist and Botsford 2011), maintain the high reproductive potential that large adults possess (Kalvass and Hendrix 1997, Shears et al. 2012, this study) and maintain the recruitment benefit provided when young urchins (Tegner and Dayton 1981) and other species of interest (e.g., abalone; Rogers-Bennett and Pearse 2001) shelter under large urchins. The potential effectiveness of strategies aimed at maintaining the abundance of large individuals are further supported by *S. franciscanus*' potential

lifespan of over 100 years (Ebert and Southon 2003) and a decreasing susceptibility to predators as they grow (Tegner and Dayton 1981). It may take a decade or longer for MPAs to increase urchin predators, reduce urchin abundance, and then increase macroalgal communities (Guidetti and Sala 2007, Babcock et al. 2010, Salomon et al. 2010, Leleu et al. 2012). In cases such as this, where the extents of barrens within and/or around an MPA are substantial, kelp forest habitat restoration may provide a "jump start" to the ecosystem changes that are associated with long established MPAs, potentially providing more rapid recovery of other organisms that would benefit from established macroalgal communities. Increases in kelp biomass as a result of restoration, will also likely increase drift kelp and associated dissolved organic matter in areas adjacent to restoration sites, important trophic resources for consumers both in and around kelp beds (Harrold and Reed 1985, Duggins et al. 1989, Tegner and Dayton 2000, Steneck et al. 2002, Graham 2004, Graham et al. 2007). By implementing a combination of management tools (e.g., MPAs, kelp restoration), resource managers may be able to mitigate the socioeconomic impacts of implementing any one management strategy in isolation, while providing greater overall ecological benefits.

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