Vol. 648: 51–65, 2020
https://doi.org/10.3354/meps13437

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published August 27

# Biogeographical variation in the distribution, abundance, and interactions among key species on rocky reefs of the northeast Pacific

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ABSTRACT: Macroecological research over large latitudinal gradients can reveal broad-scale patterns that provide context for local-scale studies and insight into relevant scales of variation in community structure. Grazing by sea urchins is one of numerous physical and biotic factors that leads to geographic variation in community structure on rocky reefs worldwide. We describe patterns of abundance, distribution, and trophic interactions of urchins and their predators on subtidal rocky reefs across much of their range in the northeast Pacific Ocean. Surveys and tethering experiments were conducted between Point Conception, California, USA, and Bahía Asunción, Baja California Sur, México, including both fished areas and marine protected areas (MPAs). Variability in abundance was greatest at the smallest spatial scales (transects and sites) rather than the largest spatial scale (regions); however, we found correlative evidence of region-wide top-down control in which higher densities of predators (primarily spiny lobsters) led to increased abundances of kelp *Macrocystis pyrifera*. Similarly, urchin survival varied regionally, with survival rates increasing from south to north. The effect of MPAs was less clear: species abundances varied between individual MPAs, but there were no clear differences in urchin survival between MPAs and fished areas. Community structure of rocky reefs in this region varies substantially among sites and appears to be driven in some locations by predators and in others by factors that obscure the importance of trophic interactions. Our study provides empirical evidence of the variability in top-down forcing in these communities and cautions against making broad generalizations based on inferences from local-scale studies.

KEY WORDS: Kelp forest · Sea urchin · Sheephead · Spatial variation · Spiny lobster · Tethering

## 1. INTRODUCTION

Understanding the ecological consequences of predation and herbivory has long been a primary focus of ecological research, and small-scale laboratory and field studies have demonstrated the ability of these interactions to strongly influence community structure in a variety of systems (Lubchenco 1978, Proulx & Mazumder 1998, Gelwick 2000, Schmitz 2003). However, the strength and even direction of species interactions is rarely homogenous across space, which can lead to geographic variability in community structure (Sanford et al. 2003, Wieters et al. 2008). As a result, increasing the spatial scale of field research may have drastic effects on the interpretation of ecological patterns (Wiens 1989, Levin

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1992). For example, the ability of predators to drive cascading effects across trophic levels on foundational oyster reefs can vary widely across space, often as a result of linkages between biological and physical processes (Kimbro et al. 2014, Grabowski et al. 2020). In turn, this biogeographic understanding can improve conservation and management efforts by providing nuanced insight into the context-dependency of species interactions across latitude or environmental gradients. On temperate rocky reefs, outcomes of the establishment of marine protected areas (MPAs) can depend on pre-reserve harvest pressure, wave exposure, reserve size, and habitat availability, among other factors (Micheli et al. 2004, Shears et al. 2008, Barrett et al. 2009, Young et al. 2016b). Large-scale biogeographic context can thus provide insight into ecological responses to increased abundance of predators within individual reserves and the potential for cascading effects on community structure (Hamilton et al. 2010, Shears et al. 2012).

Many nearshore marine species have heterogeneous spatial distributions that vary over smaller spatial scales (<100 km) (Sagarin & Gaines 2002, Gilman 2005). These patchy distributions are driven by numerous factors, including habitat heterogeneity (Sagarin et al. 2006, Blanchette et al. 2008), larval recruitment (Wares et al. 2001, Gaines et al. 2009, Herbert et al. 2009), and local adaptation (Kuo & Sanford 2009, Kelly et al. 2012). Interactions among these factors make species abundance patterns context-dependent at small scales and can lead to 'hot' and 'cold' areas of abundance over large latitudinal gradients, even within similar community types (Brown 1984, Sanford & Bertness 2009). These biogeographical patterns of abundance can be particularly important for species that have disproportionate effects on community dynamics. Variation in the abundance of predators and prey within otherwise similar communities can alter interaction intensity and outcome, leading to variation in community structure. This variation has been documented in multiple marine systems (Dethier & Duggins 1988, Estes & Duggins 1995, Jenkins et al. 2005, Sanford 2014), suggesting that a biogeographical perspective of species abundance patterns is vital to understanding the generality of species interactions across space.

On temperate subtidal rocky reefs, a complex combination of physical and biological factors leads to variation in community structure (Dayton 1985, Pinnegar et al. 2000, Steneck et al. 2002, Schiel & Foster 2015). The distribution and abundance of understory and canopy-forming kelps, the dominant algae on these temperate reefs, can be controlled by a variety of oceanographic factors, including water temperature (Hernández-Carmona et al. 2001, Wernberg et al. 2010), nutrient availability (Dayton et al. 1999, Johnson et al. 2011), and physical disturbances (Seymour et al. 1989, Young et al. 2016a), particularly during El Niño–Southern Oscillation events (Edwards & Estes 2006). Herbivory and the forces that regulate herbivore populations also strongly influence kelp abundance (Harrold & Pearse 1987, Sala et al. 1998). In particular, predators may exert top-down control on temperate reef communities by consuming sea urchins, the primary grazer of habitat-forming kelps, thereby promoting macroalgal persistence (Shears & Babcock 2002, Pederson & Johnson 2006, Watson & Estes 2011, Ling & Johnson 2012).

The primary foundation species on temperate rocky reefs from central California, USA, southward is the giant kelp *Macrocystis pyrifera*. Food web structure in this region involves consumption of giant kelp by red urchins *Mesocentrotus franciscanus* and purple urchins *Strongylocentrotus purpuratus*, 2 abundant grazers with similar ecological niches (Dayton 1985, Shears et al. 2012). Purple urchins are relatively more abundant, while the larger bodied red urchins are the target of a large commercial fishery in both California and México (Teck et al. 2018). Both sea urchins are consumed by 3 major predators: the California spiny lobster *Panulirus interruptus*, the sunflower star *Pycnopodia helianthoides*, and sheephead *Semicossyphus pulchur*, a labrid fish species (Tegner & Levin 1983, Dayton et al. 1998, Hamilton & Caselle 2015). While local-scale manipulative experiments have demonstrated the role that spiny lobster and sheephead can play in regulating urchin densities (e.g. Cowen 1983, Tegner & Levin 1983, Dunn & Hovel 2019), most of the evidence has been correlative in nature and comes from surveys or observations in a few areas, particularly the Point Loma kelp forest near San Diego, California (Dayton et al. 1998, 1999), and the kelp forests surrounding the northernmost California Channel Islands (Behrens & Lafferty 2004, Halpern et al. 2006, Hamilton & Caselle 2015). The 2 manipulative experiments that have explicitly tested for population regulation of sea urchins in this region have found little support for broad top-down control by predators (Nichols et al. 2015, Dunn & Hovel 2019), though these studies were limited in their spatial scope. Broader geographic surveys of trophic interactions within the region have demonstrated high levels of spatial variability in prey selection by predators and variation in community-level impact (Hamilton et al. 2011, Guenther et al. 2012), reinforcing the need for a more biogeographical perspective to interpret species abundance patterns on subtidal reefs in the temperate northeast Pacific Ocean.

Here, we describe patterns of abundance, distribution, and trophic interactions of sea urchins and their predators on subtidal rocky reefs at sites spanning 7 degrees of latitude along the coastlines of California, USA, and Baja California, México. Our goal was to provide biogeographical context to the disparate interpretation of the importance of ecological processes at various sites in structuring these communities (Edwards 2004, Foster & Schiel 2010). Similar to the local–regional pattern models described by Connell & Irving (2008), we expected to find one of 3 possible community-level patterns: (1) evidence of strong predatory control of herbivorous urchins (top-down control) via significant negative associations between predators and prey across the entirety of the study area; (2) a latitudinal gradient in species abundance indicative of broader oceanographic control; or (3) a high degree of site-level variability precluding broad generalizations about the forces structuring rocky reef communities. In addition, we worked inside and outside of MPAs in California to assess whether MPA establishment has resulted in changes in abundance or interactions among key rocky reef species.

## 2. MATERIALS AND METHODS

### 2.1. Study region and survey design

Our study was conducted at 20 rocky reefs spanning over 1000 km (from approximately 34–27° N) between Point Conception, California, USA, and Punta San Roque, Baja California Sur, México (Table 1, Fig. 1). This range encompasses the majority of the geographic distribution over which these species co-occur, with the biogeographical boundary at Point Conception (Burton 1998, Gaylord & Gaines 2000) acting as the northern end of significant densities of both spiny lobster and sheephead. The southern end of our study region represents the limit of the contiguous range of *Macrocystis*-dominated nearshore benthic habitats of the NE Pacific (Edwards 2004). We used a hierarchical sampling design to survey how variability in species abundance differed among spatial scales (Hughes et al. 1999, Edwards 2004). Our 20 study sites were divided *a priori* into 4 regions (Table 1): Southern California (SoCal) North, SoCal Mid, SoCal South, and Baja California. The study sites and regional groupings were selected based on an attempt to sample across the entire interacting range of the species of interest. However, because

Table 1. Survey sites and number of 30 m transects completed between 2009 and 2011. Each site is nested within a corresponding region. Marine Protected Area (MPA) status denotes the presence of full no-harvest California State Marine Reserves at sampling sites; for MPA sites we show the initial year of protection in parentheses. Two sites (Woods Cove in Laguna Beach and Broad Beach in Malibu) were provided this protection in 2011 at the end of the study but are considered non-reserve sites here. Site abbreviations are in parentheses after the site name

| Region | Site | Lat. (N) | Long. (W) | MPA (year) | Transects | Tethering |
|---|---|---|---|---|---|---|
| SoCal North | Tajiguas (TA) | 34° 27.68′ | 120° 05.65′ | No | 4 | Y |
| | Harris Point (HP) | 34° 04.12′ | 120° 21.63′ | Yes (2003) | 4 | N |
| | Cuyler Harbor (CH) | 34° 03.15′ | 120° 20.82′ | No | 4 | N |
| | Brockway Point (BP) | 34° 01.48′ | 120° 07.05′ | No | 4 | N |
| | Carrington Point (CP) | 34° 02.36′ | 120° 02.85′ | Yes (2003) | 4 | N |
| SoCal Mid | Yellowbanks (YB) | 33° 59.56′ | 119° 33.83′ | No | 6 | Y |
| | Gull Is. (GI) | 33° 57.25′ | 119° 49.05′ | Yes (2003) | 6 | Y |
| | Landing Cove (LA) | 34° 01.01′ | 119° 21.51′ | Yes (1978) | 5 | Y |
| | Lighthouse (LI) | 34° 00.85′ | 119° 21.54′ | No | 5 | Y |
| | Malibu (BB) | 34° 02.08′ | 118° 52.11′ | No | 5 | N |
| | Dutch Harbor (DH) | 33° 13.02′ | 119° 29.05′ | No | n/a[a] | Y |
| SoCal South | Laguna (WC) | 33° 31.60′ | 117° 46.22′ | No | 4 | N |
| | San Clemente Island (CP) | 32° 48.19′ | 118° 25.05′ | No | 2 | N |
| | La Jolla In (LJER) | 32° 51.20′ | 117° 16.20′ | Yes (1971) | 6 | Y |
| | La Jolla Out (QR) | 32° 51.18′ | 117° 16.58′ | No | 6 | Y |
| | Point Loma (PL) | 32° 41.53′ | 117° 16.12′ | No | 8 | Y |
| Baja California | Punta Banda (PB) | 31° 41.74′ | 116° 40.62′ | No | 6 | Y |
| | Sacramento Reef (SAC) | 29° 44.85′ | 115° 46.80′ | No | 6 | N |
| | Punta Eugenia (PE) | 27° 51.55′ | 115° 03.80′ | No | 4 | N |
| | Punta San Roque (PSR) | 27° 10.17′ | 114° 25.40′ | No | 4 | N |

[a] Density data at San Nicolas Island for all species used with permission from the long-term US Geological Survey subtidal monitoring program at San Nicholas Island. Data can be found in Kenner et al. (2013)

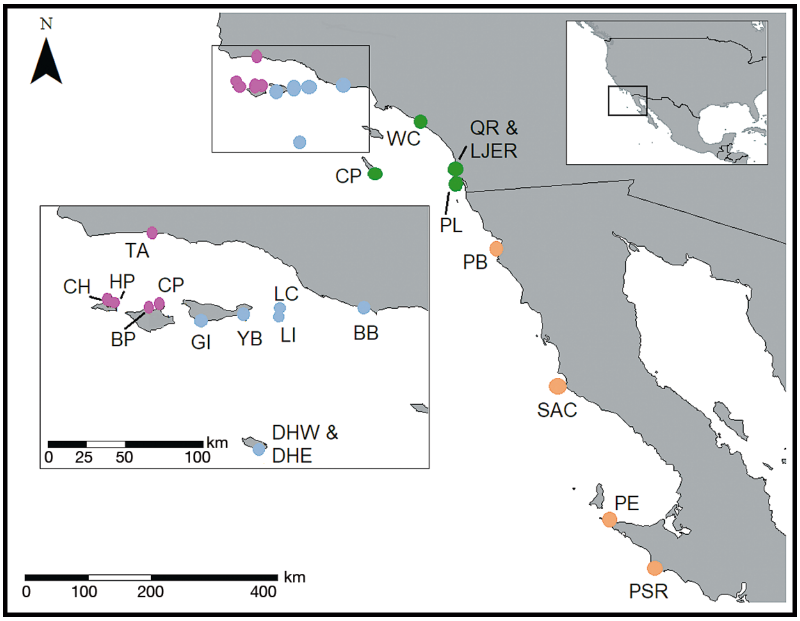

Fig. 1. Study area, demonstrating the hierarchical sampling design from Point Conception, California, USA, to Punta Eugenia, Baja California, México. Sites are designated by circles although some circles cover multiple sampling sites (see inset map). Sites are color-coded to region: purple: SoCal North; blue: SoCal Mid; green: SoCal South; orange: Baja Mexico; site abbreviations given in Table 1

subtidal reef structure is not contiguous across the entire study area, sampling locations were not perfectly spaced across the region, and MPA locations are not randomly placed. At locations with existing MPAs, we established sites inside and outside each MPA at the closest comparable reef structure within a few km of the MPA boundaries. In order to make relevant comparisons between subtidal rocky reefs at each site, we collected data at locations that shared physical and oceanographic characteristics. All survey locations within each site had open exposure to prevailing wind and swell conditions, and all surveys took place in 5–20 m of water and in areas of reef with >1 m of vertical relief along any 30 m line within a 700 $m^2$ circular area. Subtidal field surveys were conducted each year from 2009–2011, although every site was not assessed each year ($n = 2$–8 transect surveys $site^{-1}$; Table 1). To account for possible temporal changes in species abundance, we attempted to visit sites haphazardly during different seasons over the study period. While annual variation in abundance of the surveyed species may occur due to changes in harvest pressure (open seasons or market prices) or due to emigration or immigration within local areas, we observed no state shifts in community assemblage (e.g. shift from kelp forest to urchin barren habitat) at any site during the 3 study years. Consequently, we pooled survey data across years for analysis.

We varied the area surveyed among species to account for differences in their densities. Sea urchins (red *Mesocentrotus franciscanus* and purple *Strongylocentrotus purpuratus*) were counted along 30 × 2 m transects (sample area = 60 $m^2$) by a pair of divers carefully searching under all rock ledges and within reef crevices. However, the habitat was not otherwise modified to find urchins (i.e. boulders were not overturned). We therefore likely undercounted juvenile and newly recruited (<1 cm) urchins. We measured the test diameter (TD; cm) of a sub-sample of urchins of both species that were encountered along each transect, except for transects at San Nicolas Island. Those data are not the focus of the present paper, but we have plotted them for reference (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m648p051_supp.pdf). California spiny lobsters, sunflower stars, and *Macrocystis* greater than 1 m tall were counted along 30 × 8 m transects (sample area = 240 $m^2$). Sheephead were counted within paired 2 × 2 × 30 m corridors (240 $m^3$) that extended above the transect line and mirroring the bottom contours. Survey data (density and size) are available via the Zenodo data repository (doi:10.5281/zenodo.3952919). Sea surface temperature (SST), which is strongly associated with primary production, chlorophyll biomass, and nutrient levels in this region (Edwards & Hernández-Carmona 2005, Edwards & Estes 2006) was used as a proxy for oceanographic factors that might influence species abundances and thus community patterns (Zimmerman & Kremer 1984, Blanchette et al. 2008). We obtained SST values from an Advanced Very High Resolution Radiometer sensor as part of the Global Area Coverage stream provided by the US National Ocean and Atmospheric Administration. Temperatures were averaged monthly (2009–2011) from data within 1 $km^2$ pixels of each sampling site.

### 2.2. Sea urchin survival experiment

We deployed tethered sea urchins at a subset of our survey sites to test for differences in relative survival among regions and across MPA boundaries (Table 1). Tethering measures relative rather than absolute rates of survival among treatments because tethered animals cannot seek shelter from predators (Boada et al. 2015). We tethered adult purple (30–50 mm TD) and red (70–100 mm TD) urchins that were haphazardly collected at each site to avoid transplanting from other sites and to match the approximate size of urchins within the immediate area. While onboard the research vessel at each site, we tethered urchins by inserting a 1.25 mm hypodermic needle through the dorsal and ventral surfaces of the test between the oral-aboral axis and the edge of the test. Monofilament line (4 kg test) was then threaded through the needle with a ca. 30 cm tag line left for attachment to the benthos. Due to logistical challenges of working at remote sites, tethered urchins were deployed immediately; we did not observe non-predatory mortality of any urchins due to tethering. During each tethering trial, n = 10 urchins (8 purple and 2 red) were attached via cable tie to a 3.5 m length of galvanized steel chain placed in representative habitat within each site. Two replicate chains were deployed approximately 3 m apart during each trial for a total of 16 purple and 4 red urchins tethered at each site in each year. Tethered urchins were observed for 15 min immediately following deployment to record any initial predation. We then visited each site daily for 7 d or until all urchins were consumed, recording the number of urchins consumed and the predator signature of any test remains. Tethers with no urchins attached were recorded as mortality events and the predator source recorded as ‘unknown’.

We used 2 methods to estimate the source of urchin mortality in tethering trials. The first was direct observation of predation during deployment or when checking tethers over subsequent days. Second, we inspected urchin test remains, as each predator leaves a generally consistent signature of predation (Tegner & Levin 1983, Shears & Babcock 2002, Pederson & Johnson 2006). From direct observation in the field and concurrent laboratory mesocosm studies, we found that sheephead remove large portions of the test, beginning around the oral surface, often removing the urchin entirely from the tether. Spiny lobsters tend to remove smaller, slightly jagged circular openings in the oral surface of the urchin. Urchin mortality due to sunflower star predation is easily identified via a complete, clean, empty test with no fracturing. In cases where test remains were ambiguous or direct observation of predation did not occur, we classified the source of mortality as ‘unknown’.

### 2.3. Data analysis

Prior to testing, all data were evaluated for normality and homogeneity of variances using probability plots (Quinn & Keough 2002) and data were log transformed if necessary. We used separate 2 factor mixed-model nested ANOVAs to test for differences in surveyed densities of each species and SST among regions and sites. Type I (sequential) SS were used to calculate variation in each factor. For each analysis, the fixed factor ‘region’ had 4 levels (SoCal North, SoCal Mid, SoCal South, and Baja California). ‘Site’ was a random factor with 4–6 levels nested within each region (Table 1). We used variance components analyses to quantify the variance in the densities of each species and in SST that was accounted for by each spatial scale (Underwood 1997, Graham & Edwards 2001). We used separate Spearman rank correlation analyses to test for correlations between the densities of urchins and *Macrocystis*, urchins, and lobsters, and urchins and sheephead at each spatial scale. Differences in densities of each focal organism inside versus outside MPAs were examined using mixed effects models, with individual transects treated as replicates. For each of the 4 focal organisms, we fit a separate linear model including a fixed effect of MPA status (in vs. out) and treated site nested within region as a random effect to account for variability among study sites. Data from Baja California, México, was excluded from comparisons of inside versus outside MPAs, as no MPAs were sampled in this region.

We used the ‘survival’ package in R v.3.6.1 (Therneau 2019) to run survival analysis on urchin tethering data and to generate Kaplan-Meier curves to visualize the time course of urchin survival over 7 d. In initial analyses, we ran separate analyses for red vs. purple urchins, but we subsequently pooled the 2 species because survival trends were nearly identical between them. We ran separate survival analyses to test for effects of region and MPA status (in vs. out). Though we initially planned to compare urchin survival among all 4 regions, we were only able to tether urchins at one site in each of the Baja California and SoCal North regions. We combined data from these 2 sites with the SoCal South and SoCal Mid regions, respectively, and tested whether urchin survival time differed between SoCal South and SoCal Mid. Trends and statistical results were nearly identical without these 2 additional sites included. We followed survival analysis with Cox proportional hazards analysis (which allows the evaluation of effects of covariates on survival time;

Fox & Weisberg 2011) to test for interactive effects of region, predator density, and urchin density on urchin survival time. We used Akaike's information criterion to select the most parsimonious Cox model.

## 3. RESULTS

### 3.1. Surveys

We expected to find one of 3 possible community-level biogeographic patterns: (1) negative associations between predators and prey across the study area; (2) a latitudinal gradient in species abundance due to oceanographic features; or (3) high site-level variability. While SST varied predictably from north to south (see below), all focal organisms exhibited a high degree of variability at relatively small scales, either among transects within each site or among sites within each area (Table 2). In general, spiny lobster and *Macrocystis* abundances were higher in the southern end of the study region while sea urchins tended to be more abundant in the northern half of the study region (Fig. 2). Sheephead densities were variable throughout the study region with no clear broad-scale geographic pattern (Fig. 2).

The highest urchin densities were generally observed in the mid-northern sites while the lowest urchin densities were measured in the northern Channel Islands, San Diego, and southern Baja California sites (Fig. 2). Only a few small, cryptic urchins were observed at the southern end of the study area at the Punta Eugenia and Punta San Roque sites. Variability in urchin densities was largely attributed to differences among sites (59% of variation) and transects at each site (32%), while differences among regions explained only approximately 9% of the variability (Table 2, Fig. 3).

Spiny lobster densities were highest in the southern end of the study range where densities of >0.3 $m^{-2}$ were observed at the Punta Eugenia and Punta San Roque sites, moderate in the central part of the study range where densities of 0.05 $m^{-2}$ were observed at the San Diego and the southern Channel Islands sites, and lowest towards the north at the sites near Santa Barbara and the northern Channel Islands (Fig. 2). Most of the variability in lobster density was attributed to differences at the transect and site levels (57 and 35%, respectively; Table 2, Fig. 3). Surprisingly, little (approximately 9%) of the variability was explained at the regional scale (Table 2), even though a broad biogeographical pattern of increasing lobster abundance from north to south was apparent (Fig. 2).

The abundance and distribution of California sheephead was variable between sites with no clear large-scale biogeographical pattern; high densities (>0.05 $m^{-2}$) were observed at sites in all 4 regions (Fig. 2). Most of the variability in sheephead density was explained at the level of transects within each site (60%) or at the site scale (37%), while differences among regions explained very little (approximately 3%) of the variation observed (Table 2, Fig. 3).

Sunflower stars were observed infrequently at all sites and densities >0.05 $m^{-2}$ were observed rarely, only at Punta Banda in northern Baja California, San Miguel, Santa Rosa, and San Nicolas Islands in the Channel Islands. Thus, we did not conduct statistical analyses on survey data for sunflower stars.

The giant kelp *Macrocystis pyrifera* was most abundant at the southern end of the study range, where densities within the South Baja California area were almost double those observed at other sites (Fig. 2). The zero *Macrocystis* stipes observed at Lighthouse Cove on Anacapa Island was due to a

Table 2. Spatial variation in density of urchins, lobster, sheephead, and *Macrocystis* using separate 2-way mixed-model nested ANOVAs. Type I (Sequential) SS were used to estimate variances associated with each factor. **Bolded** p-values denote spatial levels of statistical significance for each species. Magnitude of effects ($\omega^2$) denote the relative amount of variation explained by each factor in each model according to Graham & Edwards (2001)

| | Type I SS | df | MS | *F* | p | $\omega^2$ |
|---|---|---|---|---|---|---|
| Urchins | | | | | | |
| Region | 6.739 | 3 | 2.246 | 3.081 | 0.057 | 0.086 |
| Site(Region) | 11.669 | 16 | 0.729 | 9.983 | **<0.001** | 0.593 |
| Transect | 5.552 | 76 | 0.073 | | | 0.321 |
| *Macrocystis* | | | | | | |
| Region | 0.314 | 3 | 0.105 | 5.513 | **0.009** | 0.105 |
| Site(Region) | 0.298 | 16 | 0.019 | 2.732 | **0.002** | 0.233 |
| Transect | 0.518 | 76 | 0.007 | | | 0.662 |
| Lobster | | | | | | |
| Region | 0.048 | 3 | 0.016 | 3.975 | **0.027** | 0.087 |
| Site(Region) | 0.068 | 16 | 0.004 | 3.767 | **<0.001** | 0.348 |
| Transect | 0.088 | 76 | 0.001 | | | 0.565 |
| Sheephead | | | | | | |
| Region | 0.0011 | 3 | 0.00035 | 2.205 | 0.127 | 0.036 |
| Site(Region) | 0.0025 | 16 | 0.00016 | 4.213 | **<0.001** | 0.368 |
| Transect | 0.0028 | 76 | 0.00004 | | | 0.596 |

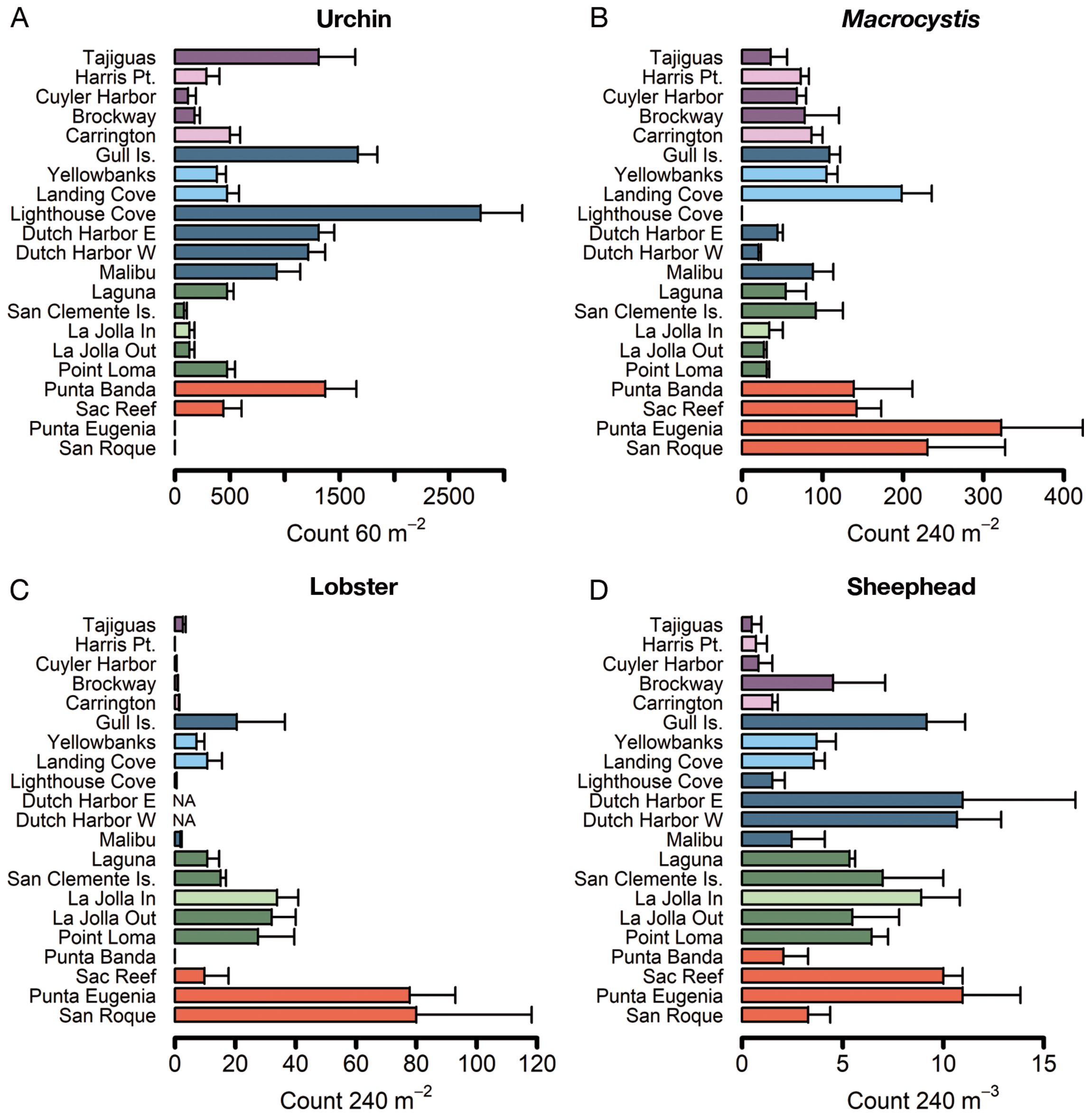

Fig. 2. Mean (+SE) counts of (A) sea urchins, (B) *Macrocystis*, (C) spiny lobster, and (D) sheephead per transect at each survey site from 2009–2011. Sites are oriented from northernmost (Tajiguas, near Point Conception) to southernmost (Punta San Roque); colors are coordinated regionally as in Fig. 1, with marine protected area sites shaded lighter within each region. Note differences in survey area covered and scale between species. *Pycnopodia* counts are not presented due to zero counts at many sites (see Section 3.1). NA in (C): no lobsters were collected at these sites

large urchin barren that persisted at this site throughout the study. Approximately 66% of the variability in *Macrocystis* density was attributed to differences among transects within each site, while differences among the 4 regions explained only approximately 10% of the variability in density (Table 2, Fig. 3).

Across the study region, mean SST tended to increase from north to south (Fig. S2), with the lowest mean (±SE) temperatures (13.17 ± 1.49°C) observed at San Miguel Island in the northern Channel Islands and the warmest mean temperatures observed at Punta San Roque in South Baja (18.14 ± 2.75°C). Consequently, SST varied significantly among both regions ($F_{3,16}$ = 45.534, p < 0.001) and sites nested within region ($F_{16,700}$ = 2.21, p = 0.004).

Across the entire biogeographic region there was a significant negative relationship between spiny lobster and urchins but not between sheephead and urchins (Table 3, Fig. 4). This correlative association was driven by the strong negative relationship between spiny lobster and urchins within the Baja region (Table 3). A negative correlation between *Macro-*

*cystis* and urchin densities was observed across the study region (Fig. 4), primarily driven by sites in the Baja and Southern California regions (Table 3).

Mean urchin density varied little between MPA and non-MPA sites ($t_{12}$ = 0.356, p = 0.728). Mean predator densities were higher within MPAs than outside of them, but densities were also highly variable (spiny lobster: $t_{12}$ = −1.722, p = 0.111; sheephead: $t_{12}$ = −0.605, p = 0.556; Fig. 5). In contrast, the density of *Macrocystis* was higher inside versus outside MPAs ($t_{12}$ = −1.948, p = 0.075; Fig. 5).

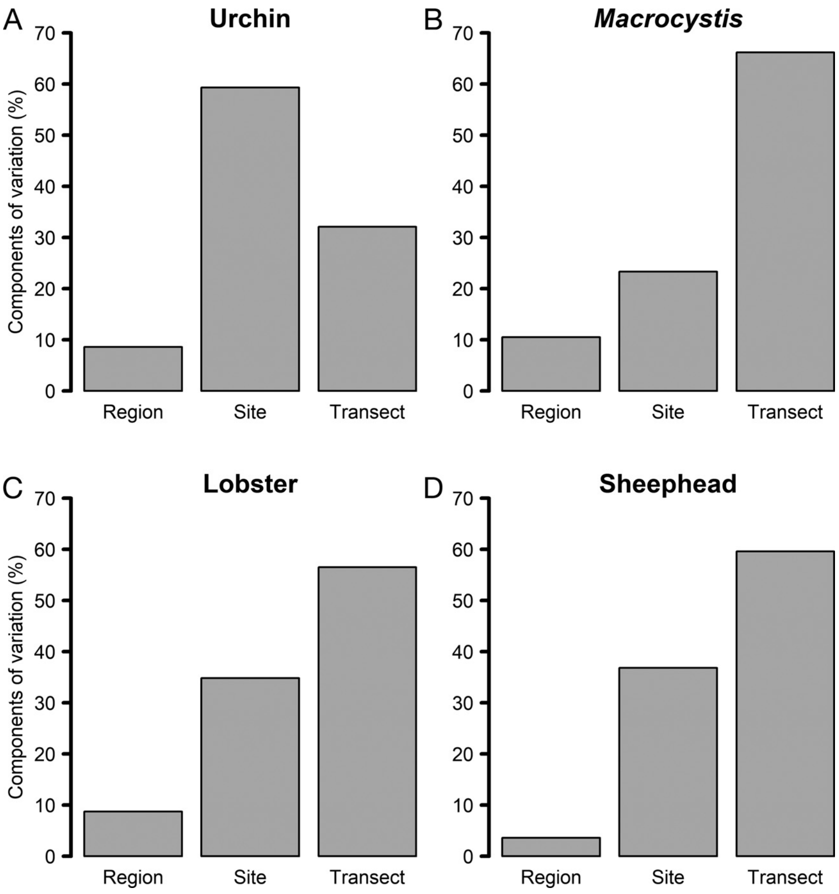

Fig. 3. Components of variation for densities of (A) sea urchins, (B) *Macrocystis*, (C) spiny lobster, and (D) sheephead across spatial scales

### 3.2. Urchin relative survival

We tethered a total of 333 urchins over the 2 yr of the study. There was a strong effect of region on urchin survival time, which was much lower in SoCal South than in SoCal Mid ($\chi^2$ = 152, df = 1, p < 0.001; Fig. 6). Urchin survival dropped rapidly in SoCal South, with most urchins consumed within 24 h. In contrast, urchin survival decreased steadily over the 7 d experiment in SoCal Mid. We also found an effect of MPA status on urchin survival time ($\chi^2$ = 4.0, df = 1, p = 0.04); however, the effect size was small, with urchin survival time averaging only 8 h higher (over the 168 h time series) within MPAs versus outside of MPAs (Fig. 6).

The best fitting Cox proportional hazards model ($\chi^2$ = 200.1, df = 3, p < 0.001) included an interactive effect of region and urchin density on urchin survival time but no effect of predator density on urchin survival time. Urchin expected survival was 4.3 times higher in SoCal Mid than in SoCal South. Though the interactive effect of region and urchin density was significant, the effects of increasing urchin density on survival were small, and trends were very similar between SoCal South ($\chi^2$ = 30.6, df = 1, p < 0.001) and SoCal Mid ($\chi^2$ = 14.2, df = 1, p < 0.001): in both regions, adding 10 urchins $m^{-2}$ increased urchin survival by <1%.

Based on diagnostics of urchin test remains, 51% of tethered urchin mortality within MPAs was attributed to sheephead and 10% to spiny lobster (Fig. S3). In contrast, at non-MPA sites predation was more evenly distributed between sheephead (27%), spiny lobster (21%), and unknown causes (36%). Only 9 of

Table 3. Association of predators and primary producers to sea urchins across the entire study area and within each of the 4 regions. Correlations determined using Spearman rank correlation analysis. All densities log($x$ + 1) transformed. **Bold** denotes p < 0.05

| Scale | Species | r | p |
|---|---|---|---|
| Across study area | Lobster | −0.404 | **<0.001** |
| | Sheephead | −0.065 | 0.520 |
| | *Macrocystis* | −0.254 | **0.011** |
| Region | | | |
| SoCal North | Lobster | 0.535 | **0.015** |
| | Sheephead | 0.021 | 0.929 |
| | *Macrocystis* | −0.118 | 0.621 |
| SoCal Mid | Lobster | 0.040 | 0.827 |
| | Sheephead | 0.214 | 0.232 |
| | *Macrocystis* | −0.492 | **0.004** |
| SoCal South | Lobster | 0.061 | 0.767 |
| | Sheephead | −0.274 | 0.175 |
| | *Macrocystis* | 0.186 | 0.364 |
| Baja California | Lobster | −0.603 | **0.005** |
| | Sheephead | −0.243 | 0.303 |
| | *Macrocystis* | −0.458 | **0.042** |

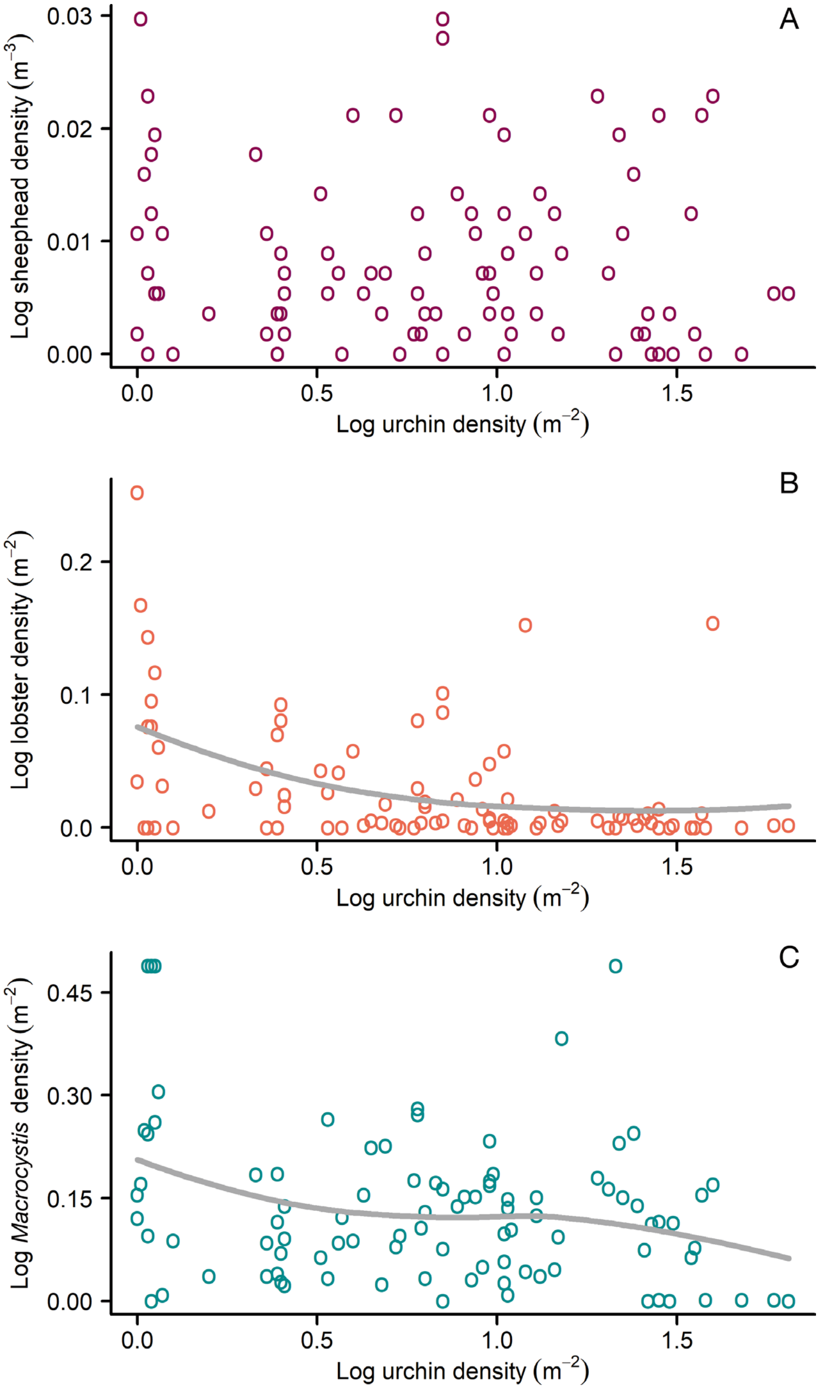

Fig. 4. Correlations between total sea urchin density and (A) sheephead, (B) spiny lobster, and (C) *Macrocystis* > 1 m in height. Data are transect-level densities with all surveys sites and years plotted individually. In (B) and (C), the grey line represents a locally weighted scatterplot smoother to visualize the relationship between (log) urchin density and (log) lobster and (log) *Macrocystis* density, respectively. See Table 3 for statistical analyses

the 333 tethered urchins were consumed by sunflower stars at 2 of the sites, although 80 % of the predation at Punta Banda, in North Baja California, was attributed to sunflower stars. Sunflower star density at this site (0.042 m$^{-2}$) was 5 fold higher than mean sunflower star density at all other sites combined (0.008 m$^{-2}$).

## 4. DISCUSSION

Observations and manipulative experiments over large latitudinal gradients can reveal broad-scale patterns that complement and provide context for local-scale studies. Our surveys and experiments, conducted across much of the overlapping range of these key interactors within northeast Pacific kelp forests, provide context for expectations of top predator release from harvest pressure in recently established MPAs within the region (Behrens & Lafferty 2004, Shears et al. 2012, Caselle et al. 2018). Our finding that much of the variation in species abundances occurred at small scales, either the site- or especially transect-level (Fig. 3), supports results from a global review of studies of subtidal and intertidal systems conducted over regional scales (>1000s of km), in which most of the variability was located at small spatial scales on the order of meters (Edwards 2004, Fraschetti et al. 2005). This suggests that local processes, such as species interactions, are important drivers of patterns of abundance and lead to ‘hot’ and ‘cold’ areas of abundance over large latitudinal gradients. However, the degree to which these patterns scale up to regional levels varied between studies and appeared both context-dependent from a biological perspective and influenced by methodological and analytical methods (Underwood & Chapman 1996, Fraschetti et al. 2005), as well as by forcing factors operating at different scales (Edwards 2004).

Despite the high degree of local-scale variability we observed here, regional-scale trends in species abundances, co-occurrences, and urchin survival were apparent. Significant negative relationships between spiny lobster and urchins, and urchins and *Macrocystis*, were observed across the study range, provid-

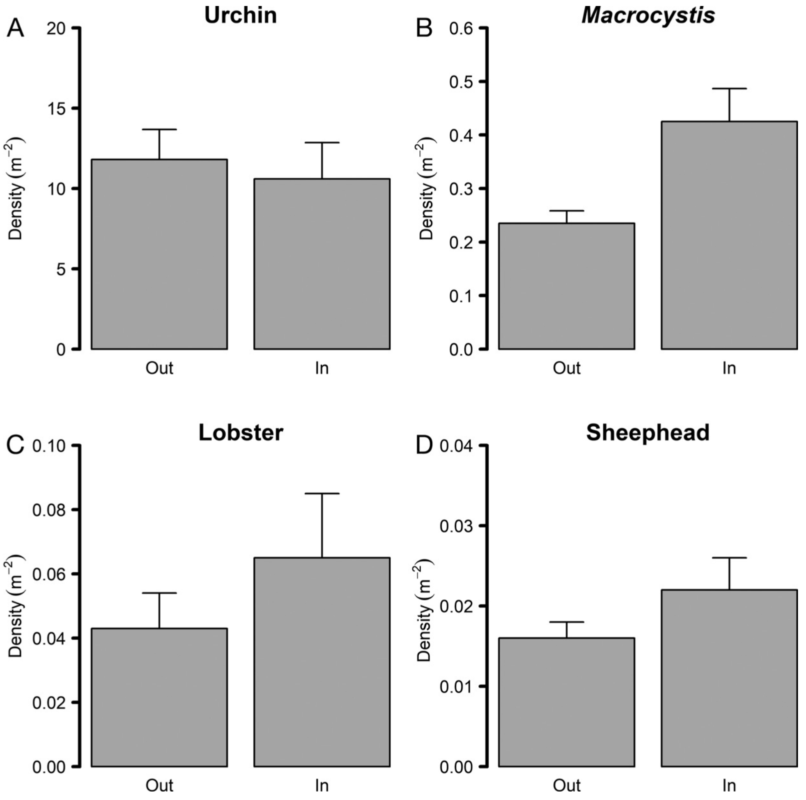

Fig. 5. Mean (+SE) densities of (A) sea urchins, (B) *Macrocystis*, (C) spiny lobster, and (D) sheephead inside and outside of marine protected areas in California, USA

ing correlative evidence of region-wide, top-down control in which higher densities of predators lead to increased *Macrocystis* abundances, perhaps via reduction of sea urchin densities. While these relationships varied in significance at a smaller spatial scale, even becoming significantly positive in some regions (e.g. lobster and urchins in the northern region), our results demonstrate the broad geographic scale upon which trophic interactions could affect rocky reef communities. We interpret this as correlative evidence that spiny lobsters have the potential to induce trophic cascades on reefs throughout the study region (Dayton et al. 1998, Pinnegar et al. 2000, Halpern et al. 2006). This contrasts results from a study in the Santa Barbara area of California that found little evidence for fishing-induced trophic cascades involving lobsters, urchins, and kelp (Guenther et al. 2012). Our results, however, suggest a high degree of context-dependency, and that a variety of biological factors operating at sub-regional scales can weaken or ameliorate cascades (Guenther et al. 2012, Dunn & Hovel 2019). Importantly, the species interactions we focused on here do not operate in the absence of oceanographic factors, including temperature, nutrients, and wave exposure, which can each influence rocky reef communities in this region (Foster et al. 2006, Young et al. 2016a). A similar pattern has been demonstrated in northern New Zealand where predator–urchin–kelp trophic cascades have been demonstrated at some (Babcock et al. 1999, Shears & Babcock 2002) but not all sites (Shears et al. 2008). Shears et al. (2008) attributed these differences to among-site variation in depth, hydrodynamic exposure, sedimentation, and distance from land, which in turn can modify urchin grazing behavior, recruitment, and algal productivity. We attempted to control for some of these factors by choosing sites with similar physical characteristics across the study range. However, we did not measure physical characteristics or recruitment dynamics at each site and thus cannot evaluate the factors that may explain variability in the intensity of top-down control at local scales. One biological factor that could contribute to small-scale variability in urchin abundance is the range of movement by predators. Both spiny lobsters and sheephead exhibit relatively small home ranges on the order of 1000s of m$^2$ (Topping et al. 2005, Withy-Allen & Hovel 2013). This locally intense use of habitat could drive small-scale variation in top-down control depending on the size and sex of sheephead and lobsters found at a site (Selden et al. 2017, Dunn & Hovel 2019, Eisaguirre et al. 2020).

We hypothesized that we would find distinct differences in species abundances between the northern and southern end of the study range, with gradual shifts in abundances indicative of bottom-up control in this system triggered by oceanographic patterns. Our proxy for physical drivers of species distribution was SST recorded daily over the 3 yr study period. Within the study range, SST is negatively correlated with oceanic nutrient levels (Edwards & Estes 2006), and during periods of prolonged high temperatures kelp can begin to senesce (Hernández-Carmona et al. 2001) and urchin reproductive output can decrease (Basch & Tegner 2007). While we did observe the expected gradient of increasing SST from north to south, this was not matched by corresponding patterns of abundance of our focal species. This does not indicate that abiotic factors are unimportant in structuring these communities over larger scales; in fact, they

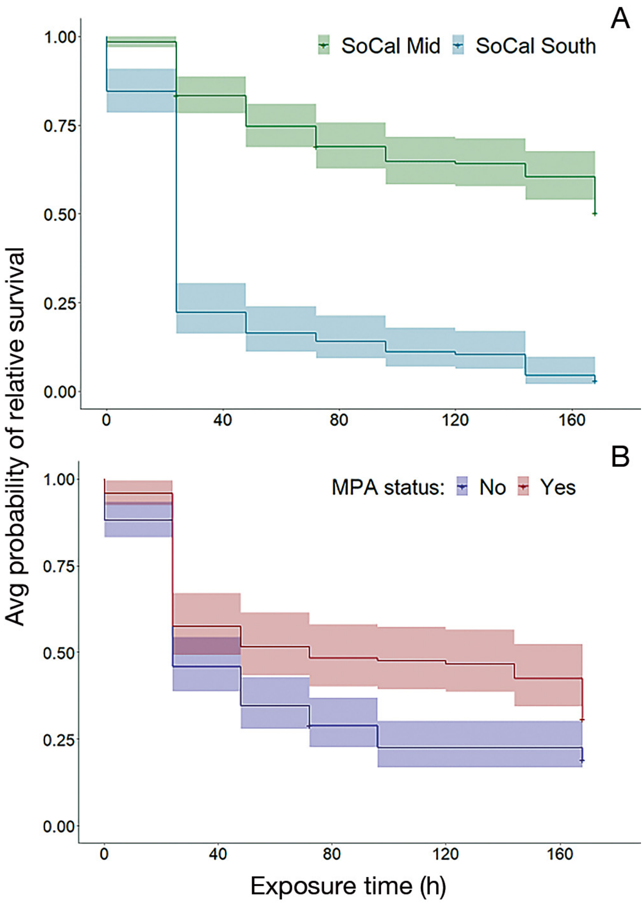

Fig. 6. Survival analysis of tethered sea urchins (red and purple) (A) within the SoCal South and Mid regions, with 2010 and 2011 trials pooled, and (B) across marine protected area (MPA) status. Shaded areas denote 95% confidence intervals

have been demonstrated to do so (Edwards 2004, Graham et al. 2007, Connell & Irving 2008). Rather, SST may not be the strongest driver of these communities at every scale. Alternative factors operating at more local scales, such as current patterns that regulate larval dispersal (Wieters et al. 2008, Gaines et al. 2009) or competition, consumption, and anthropogenic effects (Dayton et al. 1984, Graham 2004, Lafferty 2004) can also be predictive of community structure. For sea urchins, low abundances at the southern end of their range along the Vizcaíno Peninsula in Baja California, México, could be a result of decreased reproductive output in warmer waters (Hernández et al. 2004, Basch & Tegner 2007), though locally intense upwelling leads to variable SST in this region.

Most of the species surveyed in this study are the target of commercial and recreational harvest in both México and the USA. This spatially variable anthropogenic effect adds an additional layer of complexity to interpreting patterns of distribution across the study area and was not included in our analysis. Other factors that also could drive regional-scale patterns of abundance differed among the trophic levels. Sheephead densities generally decreased at the northern end of the study area, although overall regional scale trends were less apparent than for other focal species. Our estimates of sheephead density over this latitudinal gradient were similar to those observed more than 10 yr prior by Caselle et al. (2011), suggesting these populations have remained relatively stable since that time period. Distribution patterns of sheephead described here were likely caused by interactions among recruitment, oceanographic conditions, prey availability, and fishing pressure (Cowen 1983, Hamilton et al. 2011, Caselle et al. 2011). *Macrocystis* was observed at all sites except the urchin barren at Lighthouse Cove at Anacapa Island, with the highest densities observed near the southern end of the study range in southern Baja California, México. At these southerly sites, many of the individuals had no more than 2–3 stipes and reached only 1–2 m from the substrate in calm conditions. This contrasts with the larger, multi-stipe plants common at most other locations. Specific recruitment events or factors that precipitated increased survival and growth of *Macrocystis* at these southern sites was not captured during this study, but it is likely that the lack of herbivores (i.e. urchins) at these sites facilitates growth and survival of *Macrocystis* and drove the negative correlation between urchins and *Macrocystis* observed across the study region.

This predator–urchin–kelp trophic chain is influenced by abiotic and biotic factors that interact in complex ways, leading to a heterogeneous seascape where regional abiotic factors may overwhelm local predatory effects at some sites while local-scale processes may drive community structure at others. For example, community structure at Punta Eugenia and Punta San Roque at the southern end of the study range is distinct from other sites. There is evidence that abundances of the interacting species in these communities are driven by abiotic factors such as temperature (Edwards & Hernández-Carmona 2005), oceanographic currents and recruitment (Wieters et al. 2008), and physical disturbance (Edwards 2004). In contrast, the 2 sites surveyed at Anacapa Island provide a dramatic example of the local-scale possibilities of top-down forcing on subtidal reef communities. Both sites are exposed to the same oceanographic factors and share a border at the eastern end of the island. On one side is Landing Cove, a long-standing MPA established in 1978, with relatively high predator abundances, low urchin abundance, and high *Macrocystis* abundance. Immediately adjacent is the fished site at Lighthouse Cove, which remained an urchin barren with few *Macrocystis* or predators throughout the study period. It is unlikely that such stark differences in community structure at this location are driven by anything other than fishing-induced reductions in predator abundance.

There is considerable evidence that implementation of MPAs on temperate reefs can lead to community-level changes via increases in predator abundance (Halpern & Warner 2002, Shears & Babcock 2002, Lester & Halpern 2008), though the time scale of community-level effects can lag direct effects of harvested species by a decade or more (Babcock et al. 2010). Our results concerning MPA effects should be interpreted cautiously due to the limited number of MPAs we could sample, particularly in the SoCal South region where we were only able to survey inside and outside of one MPA. Our data therefore do not reflect a detailed analysis of MPA effects, but rather a broad view of overall trends. Nonetheless, our results suggest that there is variability in local-scale outcomes of increased predator abundance (Hamilton et al. 2010, Shears et al. 2012). We found marginally increased abundances of predators inside versus outside of MPAs, but substantially higher *Macrocystis* abundance inside versus outside MPA sites. This is curious because relative survival of tethered urchins was similar regardless of MPA status. Non-consumptive effects of predators on urchin behavior can lead to reductions in active urchin grazing activity (Spyksma et al. 2017), potentially explaining the effect of MPA status on kelp abundance even as tethered urchins were equally likely to be consumed inside and outside of MPAs. Interestingly, the time course of urchin survival (and proportion of urchins surviving at the end of our 7 d tethering trials) was different between the sites in the southern portion of the study area and sites in the middle of the study area. This pattern is potentially related to natural urchin density; sites with higher urchin densities (generally found in the upper half of the study range) typically had higher relative survival of tethered urchins, and a relatively steady decline in relative survival through time. Southern sites with overall lower ambient urchin densities exhibited rapid and high urchin mortality, with most urchins being found and consumed by predators within 24 h (Fig. S4). This negative density-dependence of urchin mortality agrees with previous experimental work, which generally failed to find clear evidence of top-down control on rocky reefs around San Diego, California (Nichols et al. 2015, Dunn & Hovel 2019).

We recognize the limitations of using abundance data to assess patterns of variation in community structure. For example, the relative abundance of species inside versus outside MPAs may not be indicative of trophic consequences induced by reducing fishing pressure on top predators. Other factors, including the size of predators (Ling et al. 2009, Selden et al. 2017), prey size (Stevenson et al. 2016) and quality (Eurich et al. 2014), availability of alternative prey resources (Dunn & Hovel 2019), and induction of behavioral changes in urchins that reduce grazing intensity (Cowen 1983, Watson & Estes 2011, Spyksma et al. 2017) have all been demonstrated to alter the intensity and community-level consequences of trophic interactions on rocky reefs. In particular, both predator and prey body size can be strong determinants of their predation and grazing intensities, respectively, with smaller bodied lobsters, sheephead, and urchins all exhibiting reduced per capita resource consumption (Ling et al. 2009, Stevenson et al. 2016, Eisaguirre et al. 2020). The relative importance of these factors in driving trophic cascades would be most effectively teased apart using manipulative experiments replicated along a latitudinal gradient that, when combined with survey data in a comparative-experimental approach, would enhance our understanding of the emergent effects of predatory interactions at the regional scale (Menge et al. 2002, Sanford & Bertness 2009).

As we found here, almost all large-scale studies in marine systems demonstrate variability in the patterns observed between species and communities at multiple spatial scales (Hughes et al. 1999, Edwards 2004, Fraschetti et al. 2005, Connell & Irving 2008). Still, patterns emerge that provide context and direction for local-scale research while also giving insights into implementation of ecosystem-based management. We found that biogeographical variation in the distribution, abundance, and interactions among key species on temperate subtidal reefs south of Point Conception occurred primarily at small (site- or transect-level) scales. Nonetheless, broad-scale evidence of top-down forcing in this system, driven primarily by reductions in urchin grazing on giant kelp, was detectable. Our work should facilitate continued discussion about the relative importance of top-down verses bottom-up forcing in these communities (Foster et al. 2006, Halpern et al. 2006, Foster & Schiel 2010, Dunn & Hovel 2019) while cautioning against making broad-scale generalizations based on inferences drawn from local-scale studies, particularly as it pertains to management and conservation planning.

*Data availability.* Data related to this article is available online at www.zenodo.org/record/3952919

*Acknowledgements*. We thank the multitude of researchers that made a biogeographical study of this nature possible. G. Torres provided invaluable logistical and field assistance in Baja, México. The fisheries cooperativas at El Rosario and Asuncion provided panga access to sites. Vessel and site access in Southern California was provided by San Diego State University (SDSU) Coastal Marine Institute Laboratory, Paradigm Charters, J. Caselle, and PISCO (Partnership for Interdisciplinary Studies of Coastal Oceans), University California Santa Barbara, California Department of Fish and Game, and M. Kenner at University California Santa Cruz and the United States Geological Survey (USGS). Dive assistance and support was provided by M. Anghera, M. Larson, J. Coates, M. Castorani, L. Reeve, K. Withy-Allen, L. Segui, P. Carlson, and D. Stein. We thank E. Sanford for comments on the manuscript. This is contribution number 70 of the Coastal and Marine Institute Laboratory, SDSU. This study was funded by California Sea Grant, the American Association of Underwater Scientists (AAUS), the Council on Ocean Affairs, Science and Technology (COAST), and the Joint Doctoral Program in Ecology at University California Davis and SDSU.

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*Submitted: October 17, 2019; Accepted: July 21, 2020*
*Proofs received from author(s): August 20, 2019*