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Latitudinal, seasonal, and small-scale spatial differences of the giant kelp, *Macrocystis pyrifera*, and an herbivore at their southern range limit in the northern hemisphere

Abstract: Although several studies have described kelp-urchin interactions, little is known about these interactions toward the distributional range limits of these species in areas that may experience different physical conditions than at the center of the distributional range. We explored seasonal and latitudinal changes in the population structure of the giant kelp and the purple sea urchin at their southern limits in the northern hemisphere. Densities of both organisms were positively correlated, showing a significant effect of season and latitude, and were highest in the temperate kelp populations and in the spring. The near subtropical kelp populations, however, contained significantly larger urchins. Along the boundary between the kelp beds and the urchin barrens studied, no significant spatial difference was found in sea urchin size or density. However, a general pattern of increasing probability of urchin presence with distance outside of the bed was found in spring at all sites. Spring bottom temperatures were generally colder and more variable in the temperate kelp populations, potentially explaining the larger seasonal variability found there. Data suggest seasonal differences may be modulated by the environmental variability in the temperate kelp populations and support local coupling of these two organisms at their southern range limit, in spite of the particularly unique physical conditions which occur in these populations at times.

Keywords: algae-grazer interaction; bottom-up; feed line; *Macrocystis pyrifera*; range limit; *Strongylocentrotus purpuratus*.

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Introduction

Herbivory structures marine coastal systems and has been studied worldwide (Paine and Vadas 1969, Carpenter 1986, Steneck et al. 2003, Graham 2004, Pearse 2006). Researchers have emphasized grazers' effects on complex benthic communities, such as coral reefs (Hughes et al. 2007), seagrass meadows (Valentine and Heck 1999), and temperate reefs (Harrold and Reed 1985, Guenther et al. 2012). However, the effects of natural and human sources of variation in coastal marine communities near their distributional limits have received less attention, such as in the giant kelp forests along the Baja California peninsula, which may behave differently than populations at the center of their range (Ladah et al. 1999, Edwards 2004, Ebert 2010).

The Pacific coast of the Baja California peninsula encompasses a biogeographic transition zone between the temperate waters of the California Current, and subtropical waters further south. Many species of marine algae and nearshore benthic invertebrates encounter their northern or southern limits in this region. For example, many temperate species of kelps (e.g., *Macrocystis*, *Eisenia*, *Egregia*, *Pelagophycus*), abalone (*Haliotis* spp.), and the purple (*Strongylocentrotus purpuratus*) and red sea urchin (*Mesocentrotus* (previously *Strongylocentrotus*) *franciscanus*), encounter their southern limits in the northern hemisphere along this coast, making it of particular interest for research into the population dynamics of the kelp forest ecosystem.

The Baja California transitional region is greatly affected by El Niño conditions and experiences a warmer coastal temperature regime than in California. Additionally, this area has a different upwelling regime (Zaytsev et al. 2003) and a different temperature-nitrate relationship than other areas of the California Current, with greater nitrate concentrations occurring at higher temperatures (Hernández-Carmona et al. 2001, Ladah 2003, Edwards and Estes 2006). Many of these factors have been identified as potentially influencing reproduction,

growth, development, feeding, susceptibility to disease, and life span for kelps and their grazers (Hernández-Carmona et al. 2001, Behrens and Lafferty 2004, Lester et al. 2007b, Matson and Edwards 2007), potentially altering traditionally understood patterns in their interactions established for more northern temperate populations.

Authors have previously suggested that populations of giant kelp and sea urchins are coupled in nature (Breen and Mann 1976, Dayton et al. 1992, Pinnegar et al. 2000), showing similar responses to environmental changes, as urchins are closely tied to algal habitat for their primary food source (Harrold and Reed 1985, Graham 2004, Pearse 2006). However, most of this work has been performed in northern temperate populations for sea urchins and for the giant kelp, *Macrocystis pyrifera*, whereas the kelp forest populations in Baja California Sur are known to respond to and recover from warming events such as El Niño in a different manner (Ladah et al. 1999, Edwards 2004, Ebert 2010). It is difficult to predict from published information whether the populations in Baja California Sur would be locally coupled, like they are further north, due to the fact that physical conditions can be quite different near the southern limit. For example, in the near subtropical kelp forests in Baja California Sur, water column temperatures are generally warmer than in the more northern temperate kelp populations at the same depth, and nutrients are often present at greater temperatures (Ladah 2003). In addition, storm waves (potentially due to hurricanes in Baja California Sur) may further augment the effect of warmer water temperatures, low nutrients and disease (Ebeling et al. 1985); have been shown to modulate the spatial distribution of kelp bed organisms and the diversity of the community (Byrnes et al. 2011), and can override other positive effects such as nutrient availability and reduced grazer pressure (Reed et al. 2011).

Along the Baja California peninsula, as in other areas, sea urchins are voracious herbivores of giant kelp and can attack the holdfast, releasing the entire individual sporophyte, thereby causing export of the majority of kelp biomass out of the system. This loss of biomass, in turn, has a cascading effect on the rest of the community (Graham et al. 2008). In Baja California, the red sea urchin, *Mesocentrotus franciscanus* is thought to feed passively on *M. pyrifera*, while the purple sea urchin, *S. purpuratus* is a more aggressive grazer (Palleiro-Nayar et al. 2008). Moreover, urchin harvesting in the northern area of Baja California has significantly reduced the red sea urchin population, followed by the extension of purple urchins to deeper waters due to lack of competition. This feeding expansion has been observed at two islands in northern Baja California (Palleiro-Nayar et al. 2008).

The kelp forests in Baja California can be characterized geographically using general temperature regimes and fishing pressure into northern more temperate populations, similar in oceanographic climate to those in Southern California, and southern near subtropical ones, separated along the Baja California peninsula by about 300 km by the shallow sandy Vizcaino Bay, where kelp is absent. The satellite sea surface temperatures (SST) in the northern temperate populations show a monthly average (from 1991 to 1999, NOAA Coastal Ocean dataset) ranging from 12.7°C to 22.5°C, whereas the southern more subtropical populations show an approximate 3°C warm shift in temperature ranging from 15.6°C to 25.5°C. Bottom temperature within the kelp forests follows this same general pattern and is colder and more variable in the northern kelp forests, potentially due to stronger internal wave forcing (Ladah et al. 1999, 2012, Ladah 2003). The nearshore kelp forest fisheries along the Baja California peninsula can also be characterized geographically. Greater fishing pressure for sea urchin occurs in the north. In this study, the two northern kelp forests in warm-temperate waters experience cooler temperatures much more similar to those in Southern California, as well as higher fishing pressure for red sea urchin, sea cucumber, sheephead, and *Macrocystis* than the kelp forests in the south, where fishing effort is more focused on abalone and particularly lobster.

To better understand the relationship between the giant kelp and purple sea urchin along the Baja California peninsula, we focused our study at the zone where urchins congregate along the border of a kelp forest, most often called the kelp-forest boundary (Konar and Estes 2003, Gagnon et al. 2004) or the urchin front (Leighton 1966, Mattison et al. 1977, Watanabe and Harrold 1991, Abraham 2007). We refer to this area as the kelp forest "feed line", which is the term that fisherman often use to encompass both urchins and kelps in a behavioral and ecological context, ideal for exploring local coupling of sea urchin and giant kelp.

Along the kelp forest feed line, there are physical and biological patterns that emerge from previous studies in California (Dayton 1985, Foster and Schiel 1985) and more recently in Alaska (Konar et al. 2013). The area within a kelp forest is generally characterized by a reduction in the amount of light, nutrients, and current speeds along a gradient from the outside to the inside of the forest. The area outside of the kelp forest usually has low cover of crustose coralline and red algae, is well lit, has greater energy and mixing from currents, and has higher urchin density. The border of the kelp forest is often characterized by younger kelp individuals, with fewer fronds, and

less light and water motion than outside of the forest, but more than within the forest. Within the kelp forest, there are often fewer sea urchins, significantly less light and water motion, and more frondose kelp sporophytes. This feed line is thought to be very dynamic over time and space and is regulated by several physical processes, such as light, water motion, current speeds, sedimentation, nutrient availability (Dayton 1985, Gagnon et al. 2004), and particularly by biological processes, such as sea urchin grazing (Harrold and Reed 1985, Gagnon et al. 2004, Abraham 2007). Recently, however, the kelp-urchin boundary has been shown to be relatively stable over many years in kelp forests in Alaska (Konar et al. 2013).

The aim of this study was to determine how the population structure of the giant kelp (*M. pyrifera*) and the purple sea urchin (*S. purpuratus*) changed at the kelp forest feed line with: 1) season (winter vs. spring conditions), 2) latitude (two kelp forests in the north vs. two kelp forests in the south), 3) fishing pressure, and 4) water temperature, with a clear understanding that the last two factors are inherently confounded into latitude in this study, as fishing pressure and temperature both change with latitude. Although interactions between the purple sea urchin and the giant kelp have been widely studied in California, there exists no information about this interaction at the southern distributional limit for both species, where physical stress is potentially higher than in the rest of the California current system, primarily due to higher sea surface temperatures, especially during El Niño years (Ladah et al. 1999).

We hypothesized that the population structures of the giant kelp and the purple sea urchin, which appear to be coupled in California, would be decoupled from each other in the southern Baja California populations, due to the different physical conditions at the southern limit. We did, however, expect to find significant small-scale spatial differences in the sea urchin population along the kelp forest feed line (inside, at the feed line, and outside of the kelp forest), as has been found in California, as we expected urchins to congregate along the kelp forest to feed regardless of the population under study. Our results provide insight into the dynamics of algae-herbivore populations at the edge of their distributional range.

Materials and methods

To determine the effects of latitude, season, and site on kelp population dynamics and associated sea urchins, we compared four kelp forests with similar geological characteristics: Isla Todos Santos (ITS; 31.809°N, -116.800°W) and Campo Kennedy (CK; 31.702°N, -116.683°W) in northern Baja California (with high urchin fishing pressure), and Isla Natividad (IN; 27.879°N, -115.173°) and Bahía Tortugas (BT; 27.652°N, -114.877°W) in southern Baja California, very near the southern limit (with low urchin fishing pressure; Figure 1), in two different seasons, in December 2003/January 2004 (hereafter winter) and March/April 2004 (hereafter spring). We used SCUBA diving to measure giant kelp sporophyte density and fronds per individual as well as purple sea urchin density and test diameter (mm).

We used a hierarchical design to determine the effects of latitude, season, and site on the population structure of giant kelp and purple sea urchin. At least three transects (30×2 m) were taken at ~10 m depth, spaced 20 m apart, perpendicular to the feed line, with the feed line at the center of the transect, to evaluate kelp population structure (number of individuals and fronds per individual) at every sampling period at each kelp forest. Along these transects, 11 quadrats (1 m²) were used to collect purple sea urchin data, with five quadrats placed from the border toward the inside of the forest, five from the border toward the outside of the forest, and one right at the border at the kelp forest feed line (Figure 2). Urchin density was recorded in all quadrats. In order to measure sea urchin size, we collected all conspicuous purple sea urchins in
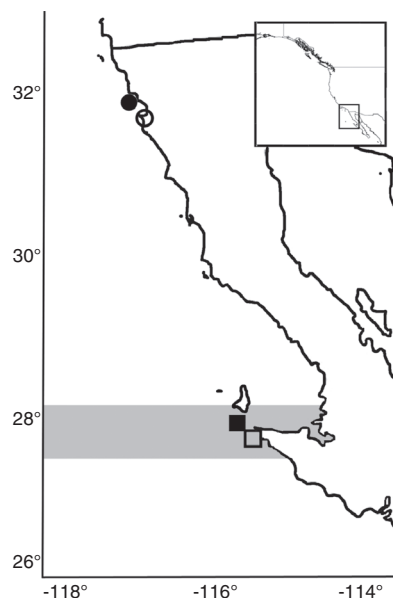

Figure 1 The Baja California Peninsula, Mexico, study region with the four sampling sites: Isla Todos Santos (dark circle), Campo Kennedy (clear circle), Isla Natividad (dark square), and Bahia Tortugas (clear square). The gray area represents the break between temperate and subtropical biogeographic regions.
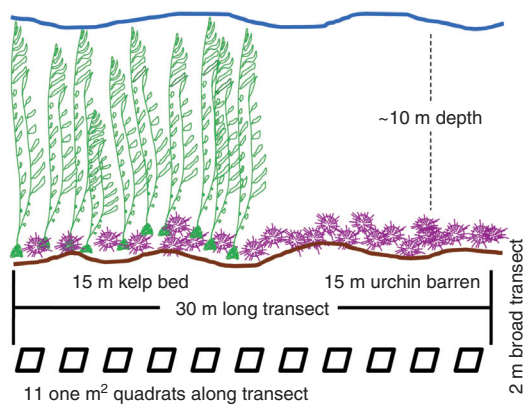
~10 m depth

15 m kelp bed   15 m urchin barren

30 m long transect

2 m broad transect

11 one m² quadrats along transect

Figure 2 Feed line sampling design between a kelp forest and an urchin barren at ~10 m depth. We collected kelp data from a 15×2 m transect. Transects were placed perpendicular to the feed line, and the center of the transect was placed at the feed line. Urchin data was collected from 1-m² quadrats uniformly distributed along the 30-m transect. Quadrat number six was placed at the feed line.

each quadrat and measured test diameter with callipers to the nearest half mm. When it was impossible to collect the sea urchins (cryptic distribution), they were only counted.

Latitudinal and seasonal variations in population characteristics of giant kelp and purple sea urchin were assessed using a nested ANOVA (p=0.05), after homogeneity of variances was confirmed with the Cochran test (Underwood 1997). Sites were divided into two different latitudes (northern and southern Baja California) as determined by differences in oceanographic characteristics (Zaytsev et al. 2003). Within each region, two kelp forests were selected: one on an island and one on the peninsula. Within each kelp forest, at least three transects were used for data collection. For sea urchin evaluations, within each transect, 11 quadrats were sampled as described above (Figures 2 and 3). This hierarchical design was
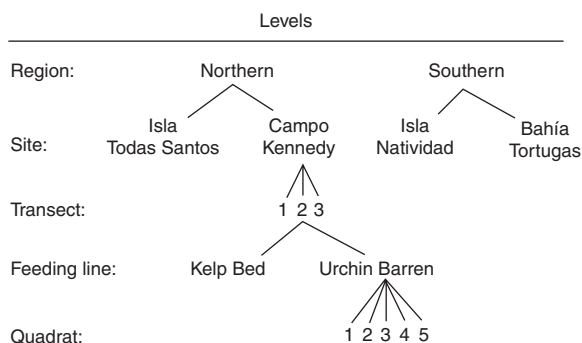

Figure 3 Hierarchical sampling design used to measure population dynamics for both: the giant kelp (*Macrocystis pyrifera*) and the purple sea urchin (*Strongylocentrotus purpuratus*). The figure refers to the number of replicates for each level. Levels are nested within the level above them. The left column indicates the scale.

performed in two different seasons, in winter and the following spring.

To describe the distribution of sea urchins along the transect, we transformed abundance data from quadrats to presence/absence data and performed a logistic regression for sea urchin probability of occurrence inside or outside the kelp bed.

To examine kelp and urchin relationships and possible differences between and among regions, we performed a linear regression with a p value of 0.05. We ran this analysis for each of the regions separately (i.e., temperate and subtropical) to compare the slopes of these relationships. In addition, we ran this analysis combining all the data to explore a regional pattern at a larger scale (i.e., Baja California).

High-frequency water-column temperatures were measured using temperature loggers deployed at 1 m above the bottom of the kelp forest at each site (Hobo temp loggers, Onset Computer Corp, Boston, MA, USA), recording every 5 min, during the spring.

Results

Urchins showed a unimodal size distribution for all kelp forests except for Bahia Tortugas (Figure 4). Overall average test diameter was 46.5±0.4 mm, ranging from 4.4 mm to 78 mm.

Latitude and season significantly affected the population structure of the giant kelp and the purple sea urchin (Table 1). Density of both species was significantly higher in the northern kelp forests than in the south, and this difference was greater in the spring than in the winter (Figure 5). Kelp frond density was also greater in the north. Urchin test diameter was, however, larger in the south, driven mainly by the BT kelp forest site, which contained the largest urchins in both seasons (Figure 5, Table 1). Site-level effects were detected for urchin density and size, but not for kelp density or frond density (Table 1).

Across the feed line, there was no significant difference in urchin density (p=0.11; Figure 6) or size distribution (p=0.88) between the quadrats within, at, or outside of the kelp border for any kelp forest studied, regardless of latitude. However, a logistic regression analysis showed that the probability of finding sea urchins inside and outside the kelp forest differed between temperate and subtropical sites (χ^2=4.39, df=1, p<0.05, Figure 7). In temperate sites, we found a higher probability of finding sea urchins outside of the kelp forest. This probability increased with distance away from the kelp bed.
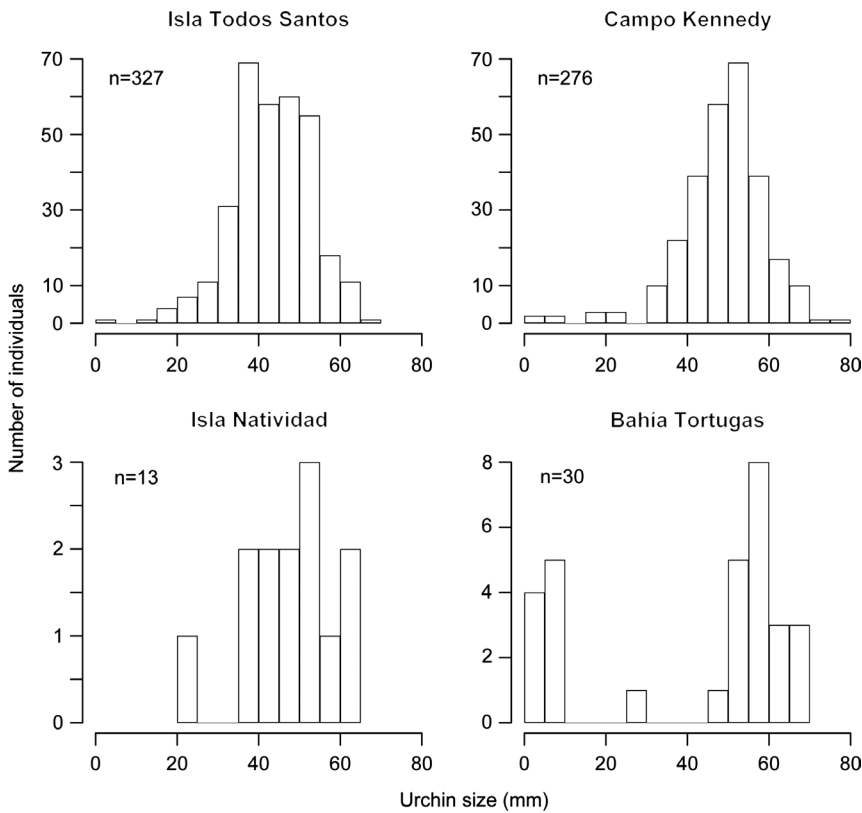
Figure 4 Purple sea urchin size distribution at different sites in Baja California.

Table 1 Fully nested ANOVA table, testing for the effect of season, location and site on urchin and kelp population characteristics.

| Effects	SS	Df	MS	F	p-Value
a) Urchin density (organisms per square meter)					
Quadrat(site*latitude*season)	7442.43	79	94.21	1.25	0.12
Site(latitude*season)	1998.09	4	499.52	6.65	<0.01
Latitude(season)	4367.98	2	2183.99	29.07	<0.01
Season	63.88	1	63.88	0.85	0.36
Error	11871.55	158	75.136		
b) Urchin size (test diameter)					
Quadrat(site*latitude*season)	3258.11	33	98.73	0.64	0.89
Site(latitude*season)	1684.59	3	561.53	3.64	0.03
Latitude(season)	136.78	2	68.39	0.44	0.65
Season	67.47	1	67.47	0.44	0.51
Error	3853.64	25	154.15		
c) Kelp density (individuals per square meter)					
Site(latitude*season)	0.603463	4	0.15	1.95	0.16
Latitude(season)	0.708574	2	0.35	4.58	0.03
Season	0.137027	1	0.14	1.77	0.20
Error	1.082339	14	0.07731		
d) Frond density (fronds per square meter)					
Site(latitude*season)	9.4966	4	2.37	0.59	0.67
Latitude(season)	99.2229	2	49.61	12.38	<0.01
Season	77.7347	1	77.73	19.40	<0.01
Error	56.0983	14	4.007		
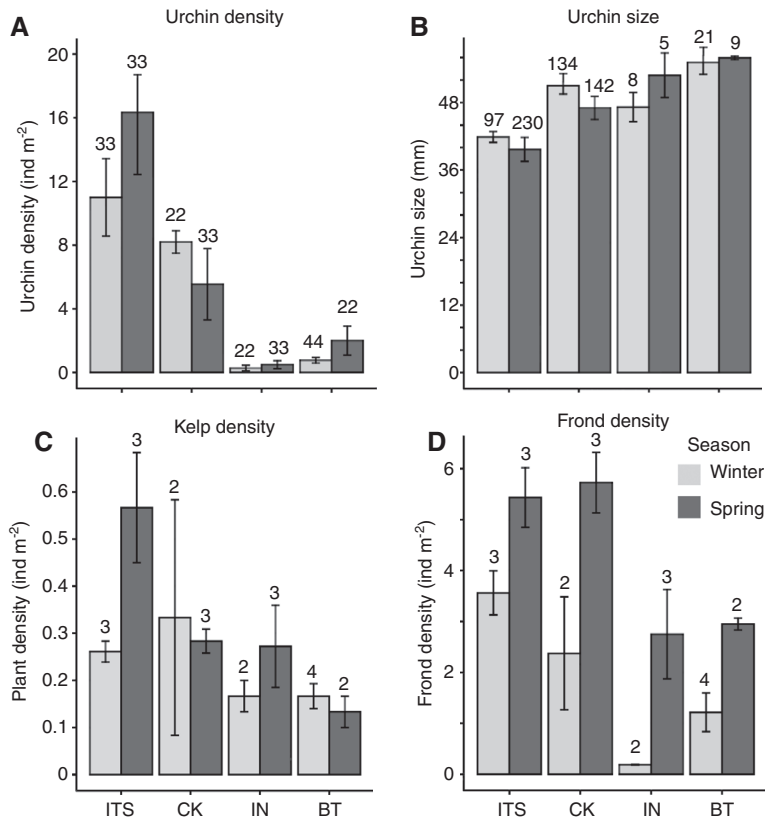
Figure 5　Purple sea urchin and giant kelp population characteristics of sampled parameters for different sites and seasons studied: (A) purple urchin density, (B) purple urchin size, (C) giant kelp sporophyte density and (D) giant kelp frond density. ITS, Isla Todos Santos; CK. Campo Kennedy; IN, Isla Natividad; BT, Bahia Tortugas. Error bars represent standard error of the mean. The number on the top of each bar represents the number of replicates.

Moreover, this pattern was stronger in spring (χ^2=4.15, df=1, p<0.05). The southern populations showed a similar, but less strong, pattern in spring. In winter, however, in the southern near subtropical populations, the pattern reversed, showing a decreased probability of finding a sea urchin outside of the kelp bed (Figure 7C and D).
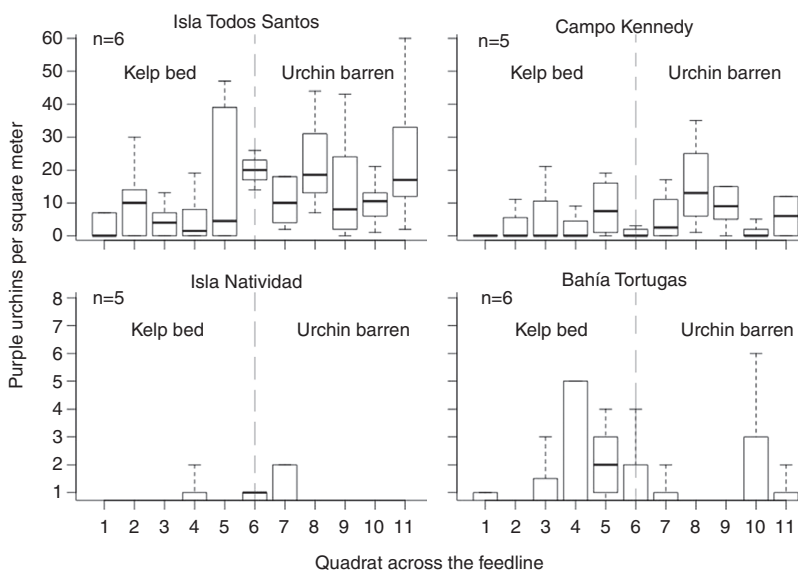

Figure 6　Purple urchin density across the feed line in each population studied. The boxes represent the minimum and maximum values, the bar in the center of the boxes represents the mean, and the whiskers represent the standard error.
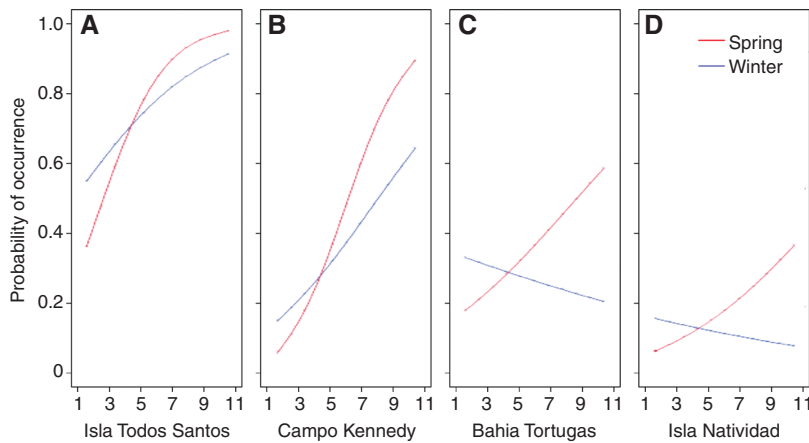
Figure 7 Logistic regression for sea urchin distribution across the feed line between a kelp bed and an urchin barren. (A) and (B) are the temperate sites and (C) and (D) the subtropical sites. Red line is winter and blue line is spring.

We found no significant relationship between kelp and urchin population characteristics when each region in Baja California (temperate and subtropical) was analyzed separately (Figure 8). However, when we grouped our data, we found a positive relationship between frond and kelp sporophyte density with urchin density, but no relationship between frond density and urchin size.

Spring water temperatures at the bottom of each kelp forest showed an average above 15°C in the southern populations and were almost 3°C warmer (>20°C at times) and less variable than bottom temperatures in the northern populations (averaging near 13°C and dropping below 11°C at times, Figure 9). March bottom temperatures varied (SD) ±0.7°C in the subtropical sites and ±1.2°C in temperate kelp forest sites. April bottom temperatures varied (SD) ±0.9°C in the southern IN kelp forest site, ±1.1°C in the southern BT kelp forest site, and ±1.4°C in the northern ITS kelp forest site. April bottom temperatures in the BT kelp forest site (average 15.2°C) and the IN kelp forest site (average 15.8°C) were significantly greater than in the ITS kelp forest site (13.1°C) (one way ANOVA, $F_{2, 27660}$=13864, p<0.001) (Figure 9).
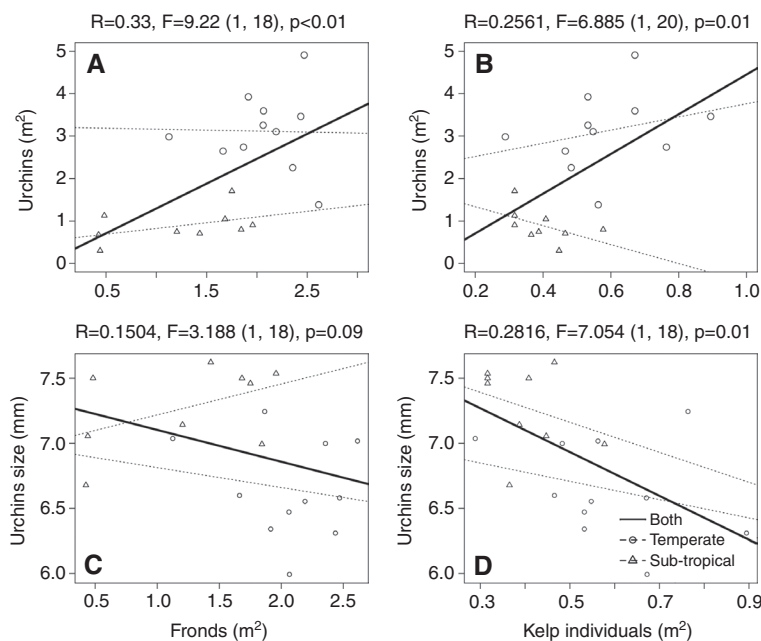

Figure 8 Relationships between purple sea urchin and giant kelp population parameters in Baja California. The statistics represent the relationships for the combined analysis.
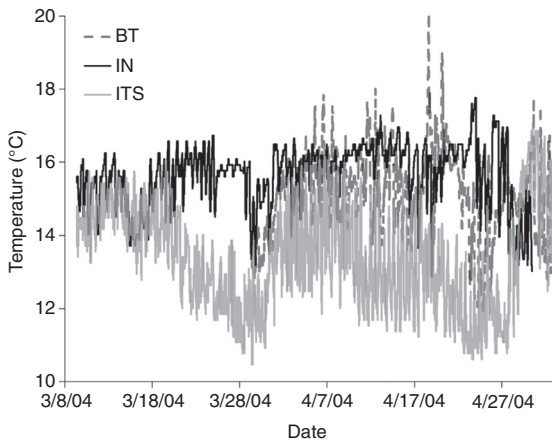
Figure 9 Bottom temperatures recorded every 5 min within the kelp forests at Isla Todos Santos (north; ITS), Bahia Tortugas (south; BT), and Isla Natividad (south; IN) during March–April 2004. Data not available for Campo Kennedy (north).

Discussion

It has been previously suggested that populations of giant kelp and sea urchins are coupled in nature (Mann and Breen 1971, Dayton et al. 1992, Pinnegar et al. 2000), and purple sea urchins are thought to be very closely connected to the habitat of algal populations for their primary food source (Harrold and Reed 1985, Pearse 2006). In the Baja California region, the purple sea urchin is often associated with giant kelp forests (Palleiro-Nayar et al. 2008, Salgado-Rogel et al. 2006). In this study we found that populations of giant kelp and urchins behaved similarly with season and latitude, suggesting that, at their southern limit in the northern hemisphere, these species are closely coupled as well.

An effect of latitude and season was found for both the giant kelp and the purple sea urchin. The amplification of this effect in spring may be attributed to increased reproduction, recruitment, and growth in this more nutrient-rich season, along with an increased food source for the purple sea urchin (Dayton 1985, Harrold and Reed 1985, Claisse et al. 2013). Alternatively, the latitudinal differences in urchin populations (particularly test diameter) could be accounted for by the differences in sea urchin abundance. To fully understand this pattern, we suggest increasing the number of samples at both latitudes for future collections. The added effect of winter storm canopy removal in the temperate northern populations, which are more wave exposed than those in the south, combined with increased recruitment cues (greater light, more nutrients), might have resulted in faster turnover

and the younger demography measured in the north, as storms can clearly modulate other top-down and bottom-up effects (Reed et al. 2011). The detected temperature difference between the two regions could also certainly modulate reproduction, growth, larval development, settlement, feeding, susceptibility to infection, and mortality for both species (Edwards and Estes 2006, Lester et al. 2007b, Blanchette et al. 2008). Populations in the north are probably less affected by stressful conditions as they are closer to the center of their range (Ladah et al. 1999, Hernandez-Carmona et al. 2001, Edwards and Estes 2006, Lester et al. 2007a, Matson and Edwards 2007), are generally less affected by climatic changes such as El Niño events, and generally experience colder temperatures (Ladah et al. 1999).

However, there is much evidence that not only temperature in and of itself, but also its variability, greatly affects many aspects of biology in seaweeds, which respond to environmental cues. For example, spore formation, growth (Mantri et al. 2010), patch stability (Wernberg et al. 2011), sex ratios in marginal populations (Oppliger et al. 2011), and edge effects (Lyons and Scheibling 2008) are all modulated by temperature variability. Water column temperature was certainly colder in the northern temperate populations, yet also more variable, possibly triggering reproduction or seasonal changes in the demography in the northern populations, whereas the temperatures in the subtropical southern populations were more stable, possibly explaining the more seasonally consistent demography there.

Because the sea urchin-kelp forest interaction is a very susceptible system in which a feed line can rapidly switch to a state of high purple sea urchin abundance with little or no kelp present, we were surprised that the feed line remained relatively stable over this study period in light of such high urchin densities, which have been documented previously (Salgado-Rogel et al. 2006). In California, a density of 10 purple sea urchins and one red sea urchin m^{-2} has been suggested to be limiting to kelp forest recruitment and stability (Leighton 1966). In addition, overfishing of lobsters, crabs, and sheephead fish in the northern populations, which are the natural predators of sea urchin, would suggest a rapid switch to an urchin barren under such high urchin densities without predator control. The maintenance of an urchin barren adjacent to a kelp bed could be explained by a drift algal food source subsidized by the nearby bed, by coralline algae or by a newly settled algal food source in the barrens (Ebeling et al. 1985). Recently, it has been shown that understory algae also play an important role in maintaining the stability of the boundaries between kelp beds and urchin barrens in

Alaska (Konar et al. 2013) and that whiplash by existing algae may prevent sea urchins from entering kelp beds. Interestingly, in this study, we did not find any evidence of progression or deterioration to an urchin barren state in spite of the high urchin densities measured in the north.

The increasing probability of finding sea urchins outside of the kelp bed detected in this study in all populations in spring has been shown for other kelp forests (Konar and Estes 2003). Sea urchin distribution may spread out and away from the kelp forest during increased nitrate conditions in spring when macroalgal recruitment may be greater outside of the kelp canopy due to increased light there. This spreading may be truncated or reversed in winter when urchins congregate nearer to the kelp forest boundary or within the kelp forest due to the dampening effects of the kelp on turbulence and waves, as well as a potentially increased food source within the kelp forest. Also, in the southern more subtropical populations, there is greater warming of bottom temperatures in winter when upwelling is greatly reduced and fleshy algal food may be limited outside of the kelp forest. The migration of sea urchins to the inside of the kelp bed in winter when other food sources may become scarce outside of the bed has been shown by Ebeling et al. (1985) and may also be related to a reduction in turbulent water flow at the edge or within the kelp bed during storms (Gaylord et al. 2007).

We conclude that the population structures of the giant kelp and the purple sea urchin along the Baja California Peninsula are coupled, as those in southern and central California, toward the center of their geographical range in the Northern Hemisphere. However, in the southern near subtropical populations, we observed that purple sea urchin and giant kelp population structures differed from those temperate populations further north, with reduced seasonal variability, larger sea urchins, and increased urchin congregation at the feed line or within the kelp forest. This could be due to an adaptation or behavioral response to the different oceanographic regime in the southern part of the peninsula, possibly modulated by different or seasonally changing food sources, differences in wave exposure, different fishing pressure affecting predators, or a combination of the above.

We were unable to tease apart the impact of fishing versus the impact of physicochemical factors in our study and can only suggest that fishing may have an additional effect, particularly in the north, where red sea urchin fishing is more common. It is near impossible to find a kelp forest in Baja California without exploitation history (either due to commercial fisheries or piracy) to tease apart these effects. The recent establishment of marine protected areas, with cooperative community involvement would help explore these questions as well as others related to climate change in the absence of fishing pressure. Ecological research in this area will benefit from detailed studies of the relative roles of life histories, recruitment, and oceanographic processes that are combined with the effects of fishing on the dynamics of these socioeconomically important species.

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