

ORIGINAL ARTICLE

Sedentary urchins influence benthic community composition below the macroalgal zone

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Abstract

Sea urchins are important ecosystem engineers in subtidal ecosystems worldwide, providing biogenic structure and altering nutrient dynamics through intensive grazing and drift algal capture. The current work evaluates red urchin (*Strongylocentrotus franciscanus*) density on fixed transects through time, individual displacement, and urchin-associated benthic community composition using a field-based approach at multiple depths (in and outside of the macroalgal zone) and replicated across sites in the San Juan Archipelago, Washington. Urchins exhibited no large-scale, temporal or directional changes in density among depths. Furthermore, 87% of individual urchins observed in repeated small-scale surveys over 3 weeks exhibited no change in position. Individual displacement was negatively correlated to drift algal capture. Evidence of sedentary behavior from the displacement surveys was supported by the sessile and mobile community composition in areas directly under *versus* adjacent to (control) urchins. The benthos under urchins had a higher percentage of bare space, crustose coralline algae, and increased density of snails, crabs and shrimp relative to associated control plots. Abundance of mobile organisms associating with urchins increased relative to control plots at the deepest survey depth (30 m), indicating a greater strength of interaction with distance from macroalgal production. This work presents evidence of food availability-related behavior in red urchins and indicates that even when sedentary, urchins have a strong influence on ecosystem structure through increasing availability of shelter and macroalgal detritus to the benthos.

Introduction

Ecosystem engineers are organisms that through their own physical structure, or the transformation of biotic and abiotic materials, modulate the availability of resources within an ecosystem (Jones *et al.* 1994). Throughout temperate reef ecosystems, sea urchins are common herbivorous grazers that exert a strong influence on benthic community composition (Steneck *et al.* 2002) by changing nutrient and community dynamics. The community effects of urchins can depend on density

(Estes & Duggins 1995; Wright *et al.* 2005; Lauzon-Guay *et al.* 2008), diet (Duggins 1981b) and behavior (Duggins 1983; Ebeling *et al.* 1985; Harrold & Reed 1985). Observations of red urchins (*Strongylocentrotus franciscanus*) in Southern California have led to a behavioral paradigm (Russo 1979; Dean *et al.* 1984; Ebeling *et al.* 1985; Harrold & Reed 1985); in general, when reef-scale food abundance is high, urchins are cryptic and sedentary. When food availability decreases, urchins adopt a mobile behavior, moving in fronts over exposed reef in search of food. The inverse relationship between food availability and

movement also has been observed in red urchins in Central and Northern California (Mattison *et al.* 1977; Rogers-Bennett *et al.* 1995), laboratory studies (Russo 1979), and other urchin species in Australia (Vanderklift & Kendrick 2005; Livore & Connell 2012b) and the North-west Atlantic Ocean (Dumont *et al.* 2006).

Fronts of mobile urchins destructively graze kelp forests and transform benthic algal community composition, greatly impacting nutrient dynamics in the ecosystem. Alternatively, urchins that exhibit sedentary behavior are generally expected to have a weak impact on benthic communities, instead allowing settlement and re-establishment of macroalgae (Duggins 1981b; Himmelman *et al.* 1983; Harris *et al.* 1984). Because of this, urchins have been called 'all or nothing' herbivores (Harrold & Pearse 1987). However, individual non-mobile urchins can structure benthic faunal communities via trophic interactions (grazing) and physical disturbance (spine scraping; Vance 1979; Sammarco 1980; Livore & Connell 2012a), as well as by providing shelter (Hartney & Grorud 2002; Gratwicke & Speight 2005). The urchin species in these studies (*Centrostephanus coronatus*, *Diadema antillarum*, and *S. franciscanus*) all have long spines relative to test diameter. The 'canopy' created within the spines thus provides habitat for smaller organisms. Furthermore, many urchins use their spines to capture and consume drift algae, thereby changing food availability to the benthos (Day & Branch 2002; Vanderklift & Kendrick 2005; Britton-Simmons *et al.* 2009). The diverse effects of urchins, from direct physical disturbance to modulating nutrient availability, result in a range of pathways by which urchins engineer benthic ecosystems (Jones *et al.* 1994).

The logistical difficulty of subtidal investigations has largely confined the study of urchins to shallow depths in the macroalgal zone, which is characterized by active production of seagrasses and seaweeds. This study depth does not reflect urchin distribution. For example, red urchins are common to depths >100 m in the San Juan Archipelago (SJA), WA (Britton-Simmons *et al.* 2012). Urchins in this system exhibit little difference in nutritional condition related to distance from zones of high macroalgal productivity (Britton-Simmons *et al.* 2009). This contrasts with studies in other regions that found a decrease in condition with increasing distance from the macroalgal zone (Rogers-Bennett *et al.* 1995; Kelly *et al.* 2012). Observations from the SJA suggest red urchins are sedentary and subsist on drift algae delivered by strong tidal currents throughout their depth range (Vadas 1968; Britton-Simmons *et al.* 2009). However, Britton-Simmons *et al.* (2009) could not rule out seasonal migration of deeper-dwelling urchins into the macroalgal zone as an explanation for their high nutritional condition, as had been suggested by Carter & VanBlaricom (2002). Based

on previous studies that showed a change from sedentary behavior to mobile behavior in response to food limitation, we hypothesized that red urchins in the SJA would exhibit large-scale, vertical migration in response to seasonal decreases of drift algal availability, their primary food source. During these coordinated movements the impacts of urchins on the benthos would be spread over a wide area owing to the seasonal movement of the population, such that the area occupied by an individual urchin would be similarly affected as nearby areas with the same substrate type.

In the current study, we used a multi-scale approach to investigate large-scale temporal migration and individual-scale ecology of red sea urchins in the SJA. Surveys were conducted at three depths (10, 20, 30 m) ranging from within to below the macroalgal zone to test the hypothesis that red urchin density will increase in the macroalgal zone following periods of low drift algal abundance (late winter; Vadas 1968; Britton-Simmons *et al.* 2009) due to upward migration of deeper dwelling urchins. These surveys were replicated across three sites (Fig. 1), separated by >15 km, and repeated surveys were conducted in each of the four seasons to evaluate temporal dynamics. Observations of individual urchins were made to test the hypothesis that displacement is related to drift algal availability. Lack of large-scale or small-scale changes in urchin density through time led to a secondary hypothesis that the benthic community under sedentary red urchins would be distinct from nearby areas with the same substrate type. To evaluate this hypothesis, we

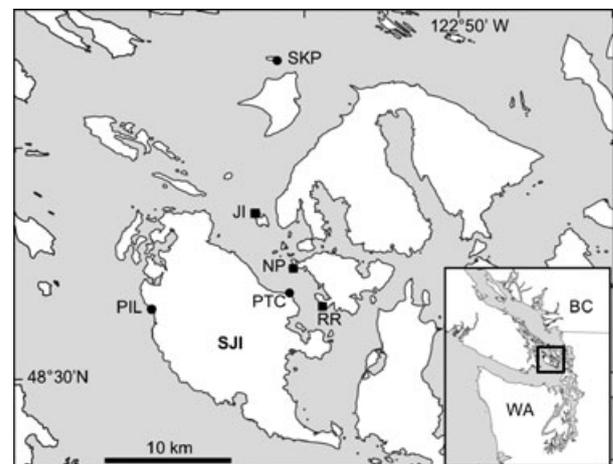


Fig. 1. Area map of the Western San Juan Archipelago (SJA) in Washington State where surveys were conducted. Urchin movement sites (circles; Pillar, Skipjack, Pt. Caution) and benthic community composition sites (squares; Jones Island, Neck Point, Roddy's Reach) were spatially segregated in order not to disturb urchins in movement study. SJI, San Juan Island, location of Friday Harbor Laboratories.

conducted photographic surveys of the benthos directly under urchins and at adjacent control plots without urchins at two depths (23 and 30 m) below the macrophyte zone. The alternative hypothesis is that the effect of migrating urchins would be dispersed over a greater area and the substrate beneath individual urchins would not differ from adjacent benthos.

Study Area

The SJA is characterized by deep channels with steep topography and large semi-diurnal tidal exchanges. In this region, macroalgae dominate the benthic community in terms of percent cover to approximately 18 m below mean lower low water (MLLW; Britton-Simmons *et al.* 2009). Between 18 and 21 m, the lower depth limit of the macroalgal zone, macroalgae become scarce and invertebrates dominate space on the substrate. The absence of attached macroalgae at approximately 20 m depth corresponds to the depth of the euphotic zone in the region (Masson & Peña 2009). Much of the macroalgal biomass produced in the euphotic zone is transported to deeper habitats as drift algae (Britton-Simmons *et al.* 2012). Red urchins in this system experience little predation due to the absence of sea otters, and primarily consume drift algae delivered by strong tidal currents (Britton-Simmons *et al.* 2009). The combination of low predation and the drift algal subsidy allows urchins to inhabit current-exposed rock outcrops, rather than cracks and crevices, as is common in some kelp forest ecosystems.

Material and Methods

Regional-scale observations

All surveys were conducted in the SJA (Fig. 1) with SCUBA. To investigate patterns of large-scale movement in the SJA region, permanent 25-m transects were installed at 10, 20 and 30 m MLLW at three sites (circles, Fig. 1): Pillar on the west side of San Juan Island (PIL), Skipjack Island (SKP) and Pt. Caution (PTC) on the east side of San Juan Island in the marine preserve maintained by the University of Washington's Friday Harbor Laboratories. The goal of this study was to monitor temporal changes in density between depths reflecting vertical migration of the population. Surveys were replicated at the three sites to quantify regional patterns of movement based on the assumption that seasonal cues would initiate vertical migration at a given depth regardless of local habitat variability. Surveys of each site were conducted prior to transect installation to locate areas aligned perpendicular to shore with urchins at the target depths. Permanent 25-m lengths of weighted line were secured

with pitons to the substrate within ± 2 m of each target depth. Fixed markers on the line divided each transect into 5-m segments. The surveyed area covered a broad range of habitats but was primarily bedrock and mixed substrates composed of unconsolidated rock and shell-hash (as defined in Britton-Simmons *et al.* 2012) and included vertical, sloping and horizontal habitat. Care was taken during transect installation not to disturb urchins in the transect area. Initial counts were made 6–8 weeks after transect installation to avoid bias from disturbance during set up.

Surveys of these transects were conducted at four periods beginning in November 2010 (fall) and ending in December 2011. In February (winter) and July (summer) 2011, three repeated surveys were conducted approximately 1 week apart to compare short- and long-term changes in urchin density. Thus, a total of nine surveys were conducted at each site over the year. During each survey, a team of divers counted all urchins within 1 m of each side of the transect line for a total of 50 m² of surveyed area per depth and 150 m² per site. To minimize interobserver variability between counts, each diver was assigned one side of the transect line and consistently counted that area, such that most counts were conducted by the same individual. Counts of adult and juvenile (<5 cm test diameter; Pfister & Bradbury 1996) red urchins were recorded separately and binned by 5-m² segment along each transect. This study focused on movement of adult urchins, therefore only the results of adult urchin counts are presented. Juvenile urchins were rare in all surveys (average 0.04 juveniles m⁻²).

Individual-scale observations

Investigating small-scale displacement and the relationship between drift abundance and movement required tracking individual urchins. Effectively tagging urchins is difficult, often invasive and can lead to mortality (Mattison *et al.* 1977; Olsson & Newton 1977; Hereu 2005). We therefore developed a method that allowed us to monitor the position of individuals over multiple weeks without causing mortality or changes in behavior that could influence density counts. We determined displacement (change in position) as a proxy for movement under the assumption that frequent random movement of individuals would result in observable displacement. Individual-scale observations were conducted within the 10-, 20- and 30-m depth transects at each site concurrent with the repeated density surveys in Summer 2011 (Fig. 1). The tracking method involved marking the substrate with a numbered weight adjacent to the first urchin encountered in each 5-m segment of transect. Repeated photographs of the marked substrate containing an urchin were then

taken each time the site was surveyed. The use of this method has two potential sources of error: identification of individuals, and movement between observations but returning to same position (homing). However, red urchins in this system exhibit multiple color morphs (red to purple) and considerable variability in the ratio of spine length to test diameter. We were able to use test diameter, color, spine length, and spine damage to track urchins in the photographs (Low 1975). Homing behavior has not been observed for urchins in this system as urchins utilize exposed bedrock and boulders instead of specific features such as cracks and crevices.

A Canon PowerShot G7 digital camera was mounted to a rigid frame to take photographs with the same 0.40×0.66 m field of view oriented to the marker. Taking photographs approximately 1 week apart over 3 weeks allowed two short-interval and one longer-interval measurement of individual-scale displacement. The position of red urchins within the field of view was determined relative to sessile organisms, substrate textures and the marker. Displacement was then calculated as the difference in the position of an urchin between the two photographs in a pair. We were interested in individual movement resulting in an urchin occupying new substrate, rather than specific rates of movement. Therefore, a scale bar (~11 cm) approximately equal to the average test diameter of urchins in the transects was installed on the camera frame as a unit of measure to score movement as <11, 11–22, 22–33, 33–44 or >44 cm. Urchins moving <11 cm were considered sedentary and all other categories were considered mobile. Urchins not present in the field of view of the second photograph were counted as 'Absent' because the exact fate of the urchin could not be determined and a distance moved could not be estimated. For functional purposes these urchins were considered mobile.

The number of individual urchin observations in the short-term photograph pairs was 29 (Skipjack), 39 (Pillar) and 21 (Pt. Caution). The percent of urchins in contact with visible drift in the photographs was also calculated for each transect. The substrate occupied by an urchin in the photographs was categorized as bedrock, boulder or mixed (unconsolidated sediment or shell-hash).

Benthic community composition

To test the hypothesis that benthic community composition differs locally in areas with and without urchins, surveys were conducted at three sites in the same region as movement surveys: Jones Island (JI), Neck Point (NP) and Roddy's Reach (RR) (squares, Fig. 1). We were particularly interested in mobile fauna associated with the spine canopy, defined as the area beneath the spines and

test, because of anecdotal observations of benthic fauna inhabiting the spine canopy. Temporal density surveys and benthic community composition studies were spatially segregated because the community research question required handling and temporary removal of the urchins from the substrate, which would have likely influenced subsequent behavior and conclusions based on density.

Surveys were conducted at two depths (23 and 30 m below MLLW) at each site between February 2011 and August 2011. These depths were selected to investigate the influence of urchins near the boundary of the macroalgal zone and at the lower depth of the density surveys. A team of divers swam along the target depth contour and photographed individual urchins at least 5 m apart to control for localized differences in benthic community. An individual urchin occupying horizontal (<45° angle) bedrock habitat was carefully removed and a photograph was taken of the benthos beneath it. An area 1 m distant from the urchin, with the same substrate type and slope angle, but devoid of urchins was selected as the no-urchin comparison (hereafter control) photograph. This was repeated until at least five pairs of photographs were taken across each depth at each site. All photographs were taken with a camera mounted on a metal quadrat with 0.25×0.30 m inner dimensions.

Photograph analysis

All photographs were color-corrected in a GNU IMAGE MANIPULATION PROGRAM (GIMP 2.6.11; Free Software Foundation, Inc., Boston, MA, USA), and imported to image analysing software (IMAGEJ 1.44p; National Institutes of Health, Bethesda, MD, USA). Photograph plots were cropped to inner quadrat framing dimensions and divided into 24 equal subunits. Subunits were quantified by eye for percent cover of sessile organisms and absolute counts of mobile organisms to finest taxonomic scale possible and totaled for each photograph. Cryptic sessile organisms that could not be identified to at least genus level were categorized into functional groups by morphotype and phylum. Between seven and 11 urchin – control pairs were analysed from each depth at each site.

Statistical analysis

Regional and individual-scale movement

To test the hypothesis that urchins exhibit large-scale temporal migrations, we used linear mixed effects models to analyse the effect of time (date) on urchin density. This method allowed us to account for the natural variation in urchin density between sites and depths in the model and specifically test for an effect of time (similar to repeated measures ANOVA). To do this, date was

considered a fixed effect, while site and transect were random effects, and transect was nested within site. Density data were square root transformed. Linear mixed effects model analyses were conducted using the package 'lme4' (Bates *et al.* 2012) in R. Two models were constructed and compared with a likelihood ratio test (LRT) to test the effects of date on urchin density: a reduced model with only the two random effects (site and transect), while a full model included these random effects and date as a fixed effect. Separate models were constructed for the five quarterly surveys (Fall 2010 and 2011, Winter 2011, Spring 2011, Summer 2011) and the three repeated surveys (in February and July 2011) to investigate changes in density related to long- and short-term durations.

Individual movement data were analysed with linear regression to evaluate trends. Post hoc pair-wise comparisons were conducted to compare the proportion of sedentary or mobile urchins among sites. Proportional data from movement studies were not transformed as both transformed and untransformed data fit assumptions of normality and homogeneity of variance.

Benthic community composition

Sessile and mobile organisms were analysed separately as they potentially exhibit very different responses to the presence of urchins. The goals of this study were focused on bedrock substrate available to sessile invertebrates. Therefore, sessile percent cover was renormalized to 100% after removing shell-hash and rubble. Rubble contributed the same percent of substrate in urchin and control plots, and therefore was assumed to be unrelated to the presence of urchins. One urchin-control pair was removed from the analysis due to the presence of >70% rubble; rubble was approximately 30% of the area in all other photos. Sessile percent cover and mobile counts were transformed for multivariate analysis using square-

root transformation with a Bray–Curtis resemblance matrix and a modified Gower resemblance matrix in PRIMER, respectively (v6; Plymouth Marine Laboratory, Plymouth, UK). Monte-Carlo estimated *P*-values are reported for tests with a low number of unique permutations. A three-way permutational multivariate analysis of variance (PERMANOVA) was run on both matrices to detect effects of site (random), depth (fixed), and treatment (fixed) on community composition. A similarity percentages (SIMPER) routine in PRIMER determined the variables that were driving differences between plots. Univariate analyses were run in R (R Development Core Team, 2011) on mobile taxa identified as primary drivers of community difference by SIMPER analysis. A Mantel test was used to compare mobile and sessile organism matrices to determine whether the communities were correlated with one another. Taxa richness and density (reported as organisms per plot) differences between urchin and control plots and depth were analysed with Welch's *t*-tests on square-root transformed data.

Results

Regional-scale movement

Urchin density on permanent transects ranged from 0.30 to 3.56 urchins m⁻² (Table 1). Standard deviations of urchin density were small for all surveys combined and generally lower for weekly surveys than quarterly surveys (Table 1). The greatest difference between minimum and maximum observed urchin density over the year was 0.62 urchins m⁻² (the equivalent of 31 urchins per 50-m⁻² transect) and never exceeded 24% of the average density for any given transect. No difference was found between the reduced (site and transect) and full (date, site and transect) linear mixed effects models describing urchin

Table 1. Density of *Strongylocentrotus franciscanus*. Summary of urchin density (m⁻²) for five quarterly transects (annual) and repeated weekly surveys (winter and summer). Annual, winter and summer transects were used in LMER analysis of change in density over time. Bold text indicates transects in which density was significantly different between winter and summer repeated surveys (*t*-test, *P* < 0.05).

Site	Depth	Annual (<i>n</i> = 5)				Winter (<i>n</i> = 3)		Summer (<i>n</i> = 3)	
		Mean	SD	Min	Max	Mean	SD	Mean	SD
SKP	10	1.48	0.11	1.34	1.60	1.62	0.04	1.60	0.02
	20	2.69	0.13	2.60	2.92	2.73	0.17	2.60	0.06
	30	1.22	0.08	1.08	1.28	1.25	0.03	1.27	0.06
PIL	10	1.85	0.15	1.66	2.08	1.80	0.05	1.86	0.04
	20	3.21	0.23	2.94	3.56	3.03	0.13	3.26	0.04
	30	1.90	0.14	1.70	2.10	1.70	0.04	1.93	0.06
PTC	10	1.54	0.09	1.44	1.68	1.49	0.06	1.60	0.02
	20	0.77	0.08	0.70	0.88	0.75	0.05	0.83	0.04
	30	0.33	0.03	0.30	0.36	0.36	0.00	0.32	0.02

density (LRT, $\chi^2 = 3.95$, d.f. = 4, $P = 0.41$), indicating that date had no effect on urchin density over the course of a year (long-term). Similarly, there was no effect of date on urchin density between weekly repeated surveys (short-term) in winter (LRT, $\chi^2 = 2.1079$, d.f. = 2, $P = 0.35$), or summer (LRT, $\chi^2 = 0.2355$, d.f. = 2, $P = 0.89$). Comparison of average density between repeated surveys in winter and summer indicated significant differences for only three transects (PIL 20 m, 30 m and PTC 30 m); however, the magnitude of change was minimal (<13%; Table 1). Furthermore, the direction of change in density was not consistent across transects (Table 1).

Individual-scale movement

In all, 58 individual urchins were tracked within the transects for approximately 3 weeks. Photographs from the Skipjack 10-m transect were not used because the substrate was obscured by poor visibility and attached macroalgae, preventing the tracking of urchins at that depth. The proportion of mobile urchins (>11 cm displacement) observed was not related to the number of days between photographs (linear regression, $r^2 = 0.059$, $F_{(1,6)} = 0.37$, $P = 0.56$). Results presented are for 89 observations of individual urchins from pairs of short duration photographs (Fig. 2). Of these, 87.6% remained sedentary (<11 cm displacement) between time points and only four of 89 (4.5%) urchins were absent from the second

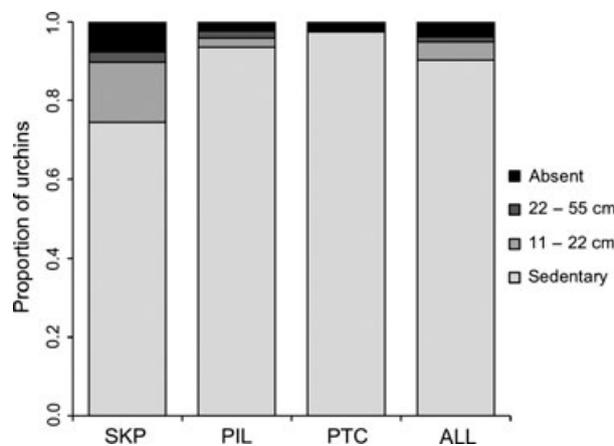


Fig. 2. Displacement of *Strongylocentrotus franciscanus*. Displacement observed for individual red urchins in small-scale movement photographs taken during Summer 2011 surveys along the 10-, 20- and 30-m transects. Displacement was scored in 11-cm bins using a scale bar on the camera frame. Displacement of <11 cm during period of observation considered sedentary; all other bins considered mobile. Number of urchins observed was 29 (Skipjack), 39 (Pillar) and 21 (Pt. Caution).

photograph (Fig. 2). Five of the remaining seven observations were of displacement between 11 and 22 cm. The proportion of mobile urchins was <26% at all sites, but was significantly higher at SKP than the other sites (pairwise t -test, SKP-PTC $P = 0.009$, SKP-PIL $P = 0.0183$, PIL-PTC $P = 0.471$; Fig. 2).

There was a significant positive correlation between the proportion of sedentary urchins and the proportion of urchins with visible drift algae in a transect (linear regression, $r^2 = 0.537$, $F_{(1,6)} = 6.97$, $P = 0.039$; Fig. 3). Of the mobile urchins, 73% had no visible drift algae. Because the individual-scale observations were conducted concurrently with density surveys, the pattern of individual movement relative to contact with drift algae could be compared with changes in density along the same transect. Although individual displacement was correlated to drift algal capture (Fig. 3), the change in urchin density over the 3 weeks of repeated regional-scale surveys in Summer 2011 was not significantly correlated to the proportion of urchins with visible drift in the transects during this period (linear regression, $r^2 = 0.167$, $F_{(1,7)} = 1.40$, $P = 0.275$). No significant relationships were found between displacement and substrate type (ANOVA, $F_{(2,5)} = 0.29$, $P = 0.757$) or depth (ANOVA, $F_{(2,5)} = 1.09$, $P = 0.404$).

Benthic community composition

Twenty-five taxa of mobile organisms and 16 functional groups of sessile organisms were found. The average

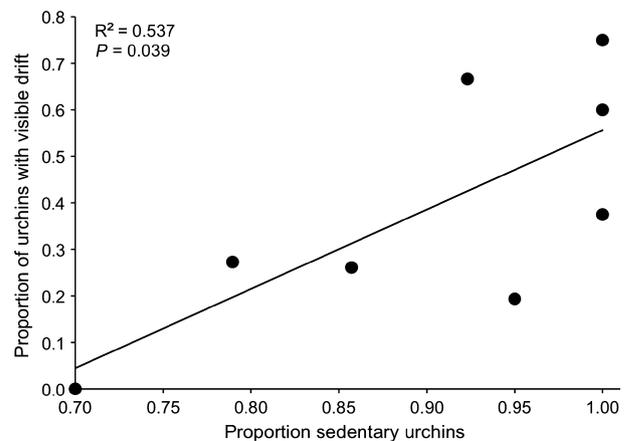


Fig. 3. Food-dependent movement in *Strongylocentrotus franciscanus*. Proportion of urchins in contact with visible drift versus proportion of sedentary urchins (observed to move <11 cm) in small-scale movement photographs. Each point represents observations from one transect, photographs from Skipjack 10-m transect were not included in analysis due to poor quality. Linear regression is significant ($P = 0.039$).

density of mobile individuals was higher in urchin (11.4 individuals per plot) than control plots (8.4 ind. plot⁻¹) across sites and depths (Welch's *t*-test, *t* = 2.45, *P* = 0.016; Table 2). One urchin plot outlier with a density of 123 *Amphissa* spp. per plot was removed from this analysis. The significant effect was driven by an increase in the difference between mobile invertebrate density in urchin and control plots at deeper sites (Table 2). Mobile invertebrate density in urchin and control plots was 12.2 ind. plot⁻¹ and 10.5 ind. plot⁻¹ at 23 m (Welch's *t*-test, *t* = 1.12, *P* = 0.267, outlier removed), and 10.6 ind. plot⁻¹ and 6.4 ind. plot⁻¹ at 30 m (Welch's *t*-test, *t* = 2.47, *P* = 0.017), respectively. Average richness of mobile and sessile taxa between plots and depths was not statistically significant (Welch's *t*-test, *P* > 0.05 in all cases). However, the richness difference between urchin and control plots was again greater at 30 m than at 23 m (Table 2).

Mobile community composition was significantly different between urchin and control plots across sites and depths (Table 3). Plot differences were consistent even though significant site and depth effects were observed (Table 3), and were most commonly driven by *Amphissa* spp. (Neogastropoda), *Trichotropis cancellata* (Mesogastropoda), *Pagurus beringanus* (Decapoda), *Pandalus* spp. (Decapoda) and *Calliostoma* spp. (Archaegastropoda; Fig. 4). These five taxa explained as much as 71.5% of the variation between plots (SIMPER). All of these taxa were observed at higher densities under urchins than in control plots except for *T. cancellata* (Fig. 4). Significant positive associations were also seen for *Loxorhynchus crispatus* (Decapoda).

There was a significant difference in the sessile community between urchin and control plots at all sites (Table 3). Sessile community composition was significantly different between depths and among sites, with a significant interaction between site and depth (Table 3). Differences between urchin and control plots were driven by the percent cover of hydroids, unidentifiable fuzz

Table 3. Results of PERMANOVA analyses of benthic community composition on counts of mobile organisms (using a modified Gowers resemblance) and percent cover of sessile invertebrates (data square-root transformed, Bray–Curtis resemblance) collected at three study sites where each analysis is a three-way design with factors Site (JL, NP and RR), depth (23 and 30 m) and plot (urchin, no urchin; see Material and Methods). Analyses use Type 3 sums of squares, fixed effects, 9999 permutations of data residuals to determine significance. Monte-Carlo generated *P*-values are presented. Significant differences (*P* < 0.05) are in bold.

Source	d.f.	MS	Pseudo- <i>F</i>	<i>P</i> (MC)	Unique permutations
Mobile organisms					
Site	2	1.491	3.093	0.0001	9874
Plot	1	3.323	10.714	0.0001	192
Depth	1	0.927	2.752	0.017	360
Site*Plot	2	0.309	0.641	0.990	9881
Site*Depth	2	0.336	0.700	0.911	9902
Plot*Depth	1	0.162	0.274	0.990	9666
Site*Plot*Depth	2	0.592	1.230	0.200	9892
Residual	100	0.482			
Total	111				
Sessile organisms					
Site	2	1841.0	5.145	0.0001	9922
Plot	1	1857.3	4.747	0.015	170
Depth	1	3104.7	4.380	0.017	170
Site*Plot	2	391.3	1.094	0.358	9927
Site*Depth	2	708.9	1.981	0.039	9932
Plot*Depth	1	189.1	0.381	0.865	6989
Site*Plot*Depth	2	496.4	1.387	0.183	9916
Residual	47	357.8			
Total	58				

(likely a combination of small hydroids and bryozoans covered in sediment or detritus), crustose coralline algae, encrusting bryozoans and solitary ascidians (SIMPER; 15.45, 14.30, 10.80, 9.85 and 9.54%, respectively). All taxa had lower percent cover in urchin plots, except for crustose coralline algae, which increased in percent cover. No correlations were observed among the quantified sessile and mobile organisms (Mantel, *P* = 0.764). Available

Table 2. Comparison of mobile and sessile communities between urchin and control plots. Density per plot and species richness are reported for mobile organisms. Available space, defined as percent of plot occupied by bare rock and crustose coralline algae, and species richness are reported for sessile invertebrates. Bold values indicate significant differences (Welch's *t*-test, *P* < 0.05).

Depth (m)	Variable	Mobile		Variable	Sessile	
		Urchin	Control		Urchin	Control
23	Density (plot ⁻¹)	12.2	10.5	% Available Space (plot ⁻¹)	21.8	8.2
	Species richness	4.4	4.6	Species richness	9.3	9.4
30	Density (plot ⁻¹)	10.6	6.4	% Available Space (plot ⁻¹)	20.5	9.0
	Species richness	4.1	3.3	Species richness	8.1	8.9
Total	Density (plot ⁻¹)	11.4	8.4	% Available Space (plot ⁻¹)	21.2	8.6
	Species richness	4.3	4.0	Species richness	8.7	9.2

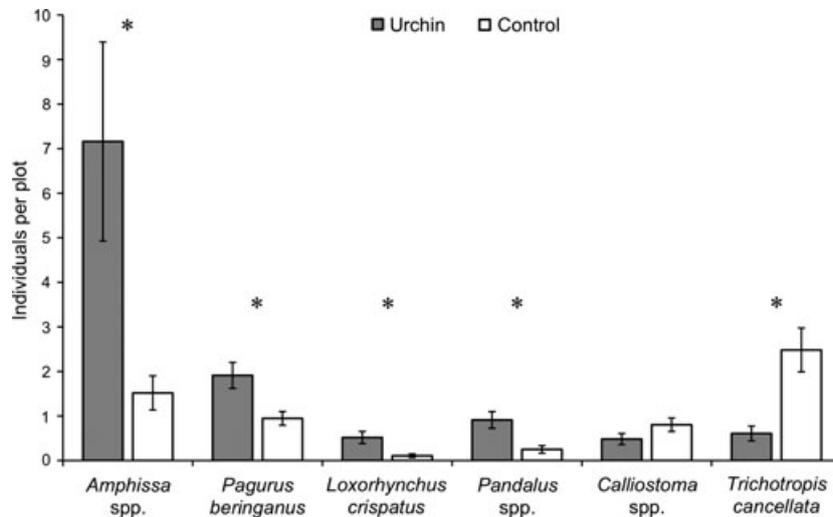


Fig. 4. Mobile organisms associating with *Strongylocentrotus franciscanus*. Mean density of mobile organisms in urchin plots (gray) and control plots (white) pooled across site and depth. * Indicates significant difference between urchin and control plot (Welch's *t*-test, $P < 0.01$). Error bars indicate standard error of the mean.

space, defined as bare bedrock and crustose coralline algae (Elahi & Sebens 2012), was significantly higher in urchin plots (21.2 versus 8.6% control, $P < 0.0001$; Table 2). This difference was greater at 23 m, yet significant at both 23 and 30 m (Table 2). Similar to mobile organisms, species richness was not significantly different between urchin and control plots (Table 2).

Discussion

Regional and individual-scale movement

The observation of consistent urchin densities at multiple depths over the course of a year leads us to reject the hypothesis that red urchins in the SJA exhibit large-scale, temporal vertical migrations. This conclusion is consistent with previous anecdotal observations from the region that suggest urchins in the SJA exhibit less movement than in other coastal regions (Vadas 1968; Low 1975; Britton-Simmons *et al.* 2009). Thus it is unlikely that seasonal vertical movement into zones with greater food resources explains the good nutritional condition of deep-dwelling urchins (Britton-Simmons *et al.* 2009). Instead, the healthy condition and the abundance of drift algae throughout the urchins' depth distribution (Britton-Simmons *et al.* 2012) suggest food is not limiting in this system and is likely contributing to the observed lack of movement. This contrasts with studies from other areas with different drift algal dynamics in which urchin movement increased and gonad weight decreased with distance from the zone of high macroalgal productivity (Mattison *et al.* 1977; Rogers-Bennett *et al.* 1995).

In Northern California, urchins at 3–5 m depth (with abundant drift algae) were characterized by higher gonad index and lower rates of movement compared with urchins at 17 m (few drift algae); the corresponding 20-fold

decrease in urchin density between depths lends further weight to the evidence for depth-related food limitation (Rogers-Bennett *et al.* 1995). A similar distribution of red urchins occurs in Barkley Sound, British Columbia, where urchins were concentrated near the macroalgal zone and seasonal movement was largely related to water motion, but potentially affected by seasonal food availability (Pace 1975). Conversely, red urchin density in the SJA did not decrease consistently between 10 and 30 m (Table 1), which is particularly interesting for a predominantly algal consumer. A larger scale study using a remotely operated vehicle showed urchin density in the SJA did not decrease appreciably until 50 m (Britton-Simmons *et al.* 2012). Even though our method (density surveys through time) cannot rule out movement (displacement) in and out of our fixed transects, the consistent urchin density at 20 and 30 m depths across time and replicate sites indicates that animals are regularly living outside of the macroalgal zone.

The small-scale photographs corroborated conclusions made from analysis of the regional-scale surveys: red urchins in the SJA exhibit very little displacement. Furthermore, individual displacement was not related to depth (*e.g.* distance from the macroalgal zone) or substrate type. More than 87% of observations were of a change in position less than the diameter of an average urchin test (Fig. 2). The greatest observed displacement of an individual in the current study was approximately 44 cm over 4 days, the distance equivalent to the daily movement of food-limited urchins in California (Mattison *et al.* 1977). We recognize that the length of time between photographs could have allowed urchins to move away from the marker and return; however, this homing behavior has not been observed in red urchins in this region, as the urchins do not utilize specific features beyond exposed rock substrates (*e.g.* crevices). The high

proportion of urchins that maintained the same position on the substrate (78 of 89 observations) provides further evidence that the consistent densities observed in the summer surveys were a function of sedentary behavior rather than localized random movement.

The method of photographing individual urchins provided drift capture data along with displacement, information previously only available from lab studies (Russo 1979). The availability of drift can alter the behavior of red urchins on a population-scale, which in turn can have significant effects on the surrounding benthic community (Dean *et al.* 1984; Harrold & Reed 1985; Rogers-Bennett *et al.* 1995). Displacement differences between sites were small and significantly correlated to drift availability; the lower proportion of sedentary urchins at SKP may have been a response to low drift availability during Summer 2011 (Fig. 3). These observations were made during summer when drift algal availability is high. The relationship between individual displacement and drift capture suggests more small-scale movement may occur during winter. However, this pattern did not translate to changes in regional density. One potential explanation stems from drift dynamics in the SJA (Britton-Simmons *et al.* 2012). Drift algal abundance in sublittoral habitats is highly variable in space and time (Vetter & Dayton 1999; Vanderklift & Wernberg 2008; Britton-Simmons *et al.* 2009) and drift can travel large distances (Kirkman & Kendrick 1997).

Red urchins observed outside of the density transects at PTC captured on average 21.2 g drift algae per urchin per day in April, June and September of 2012 with a maximum of 34.8 g drift algae per urchin per day (A. Galloway, unpublished data). These capture rates exceed average daily consumption by as much as six times (A. Lowe, unpublished data; McBride *et al.* 2004; Vadas 1968). The consistent urchin densities observed throughout the study imply that brief periods of decreased drift availability can change individual behavior, but may not last long enough to trigger behavioral changes at the regional level. In addition, feeding on sediment during winter may offset some of the decreased drift supply, thereby decreasing the need for urchins to move (Britton-Simmons *et al.* 2009). Collectively, the availability of drift, drift capture rates and relationship between individual displacement and drift capture (Fig. 3) indicate that the drift algal subsidy is sufficient to meet urchin nutritional requirements in the SJA (Britton-Simmons *et al.* 2009) and to allow urchins to remain sedentary throughout their depth range.

Benthic community composition

The comparison of benthic community composition under urchins to nearby areas without urchins supports

the hypotheses that urchins are largely sedentary in the SJA and greatly influence benthic community composition on a local scale. There was a highly significant effect of urchins on mobile and sessile community composition (Table 3). The magnitude of these differences provides compelling evidence of localized effects of sedentary urchins given the stark differences between urchin and control plots. Although the richness and type of associated taxa did not differ significantly between plots, both the density of mobile organisms and the available space were significantly higher in urchin plots. These differences in community imply an attractive effect of urchins on mobile organisms, and a disturbance effect on the sessile community.

The abundance of mobile organisms under urchins indicates the importance of the biogenic structure that urchins provide (Fig. 4). The higher mobile organism densities under urchins (Table 2) may be a function of changes in habitat availability; macroalgal canopies are completely absent at 30 m (Britton-Simmons *et al.* 2009). In shallower water, macroalgal cover (primarily *Agarum* spp.) potentially offers protection for mobile organisms from currents and predators. Below the macroalgal zone, red urchins represent the dominant above-substrate structure and therefore likely provide essential habitat for smaller invertebrates. The spine canopy of adult urchins has been shown to be important biogenic structure for fish (Hartney & Grorud 2002) and many small invertebrates (Rogers-Bennett & Pearse 2001; Nishizaki & Ackerman 2007) in shallow subtidal environments, particularly when the presence of other structures is limiting (Gratwicke & Speight 2005). Although this study focused on the urchin-associated community below the macroalgal zone, similar associations of mobile organisms with urchins have been observed in the macroalgal zone as well (R. Whippo, A. Lowe, pers. obs.). Collectively, these studies indicate the biogenic structure provided by urchins is crucial for subtidal invertebrates, including the juvenile stages of many organisms. The current work expands these observations to below the photic zone, where the lack of structure from macroalgae may increase the strength of associations among mobile organisms and red sea urchins.

The feeding strategies of the organisms associated with urchins in this and other studies suggest another important role of urchins in subtidal systems. The capture of drift algae transported from the macroalgal zone makes large pieces of algae available to benthic herbivores, including smaller *Strongylocentrotus* species (Duggins 1981a; Rogers-Bennett *et al.* 1995) and juvenile abalone in the SJA (Rogers-Bennett *et al.* 2011). In addition, urchins inefficiently digest drift algae, producing abundant fecal pellets consisting of drift algal-derived

particulate matter that may be available to a broader range of consumers than the drift algae itself (Mamelona & Pelletier 2004; Sauchyn & Schiebling 2009; Sauchyn *et al.* 2011). Below the macroalgal zone, animals rely on energy subsidies, as primary production is essentially non-existent. Drift algal capture by urchins therefore represents a localized energy source in the deep subtidal. The increased abundance of grazers and detritivores under urchins (Fig. 4), particularly at increasing depth, implies urchins play an important role in connecting the drift algal subsidy to the benthos. This relationship is worthy of further empirical study given the prevalence of red urchins in deep subtidal habitats.

Sessile communities exhibited considerable spatial heterogeneity, as differences were observed in control plots among sites and depths, along with an interaction between site and depth (Table 3). However, the sessile community beneath the urchin canopy was significantly different than nearby control plots across sites and depths (Table 3). The amount of bare space was distinctly increased and the presence of fragile organisms (including hydroids and unidentifiable fuzz) decreased in the presence of urchins. These results support the findings of previous studies showing that urchins create space and change sessile communities (Sammarco 1980; Elahi & Sebens 2012). Interestingly, the influence of urchins was often limited to the diameter of the spine canopy, such that adjacent areas were seemingly undisturbed. This pattern is consistent with the individual-scale observations suggesting little movement, as frequent random movement would reduce the likelihood of observing large differences between the substrate occupied by an urchin and substrate 1 m away. Livore & Connell (2012a) found a similar 'halo' surrounding sedentary urchins in Australia, where disturbance was limited to a small area around each urchin. While this study did not address differences in benthic community composition between sessile and mobile urchins *per se*, this work suggests an area of interest for future manipulative studies.

The current study provides evidence to support the paradigm that food availability drives urchin behavior on a regional scale, and elucidates ecological consequences of the relationship. In this system where drift algae are abundant, urchins are primarily sedentary and do not make large-scale migrations in response to food availability. They therefore create localized impacts on the benthic community. Red urchins are common throughout the coastal Northeast Pacific Ocean from the shallow subtidal to below the macroalgal zone. Their cumulative influence on benthic community composition thus contributes to community structure on a regional scale, and extends below the depths where well documented herbivory effects exist.

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