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Research Article

Changes in Abiotic Drivers of Green Sea Urchin Demographics following the Loss of a Keystone Predator

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Sea urchin population demographics can respond to changes in keystone species abundances, with the magnitude of these responses varying depending on environmental influences. In this study, sea urchin populations were surveyed across 15 Aleutian archipelago islands over a 30-year period to understand how patterns of sea urchin demography (density, biomass, and size structure) varied through different ecological regimes that were caused by changes in the abundance of sea otters, a keystone species in this system. To examine long-term changes in sea urchin demographics, four time periods across the recent decline of sea otters were examined: during sea otter presence (1987-1994), nearing absence at the end of the decline (1997-2000), 10 years postdecline (2008-2010), and 15-20 years following the loss of sea otters from the ecosystem (2014-2017). Our results show that when sea otters were broadly present, sea urchin demographics were generally similar across the archipelago, with few urchins that had large-sized bodies. During this time, bottom-up environmental controls were muted relative to top-down forces from keystone predation. However, as sea otters declined and remained absent from the system, abiotic factors became more influential on sea urchin biomass, density, and size structure. In particular, differences among island groups during these periods were correlated with variation in ocean temperature, bathymetric complexity, and habitat availability. Sea urchin recruitment also varied among island groups, corresponding to ecoregions delineated by oceanic passes across the archipelago. The functional extinction of sea otters revealed an increasing influence of abiotic forcing in the absence of top-down control. This study further highlights the importance of understanding how keystone predators regulate herbivore demographics.

1. Introduction

Keystone species strongly influence the structure and function of diverse ecosystems by regulating the demography of their prey [1–3]. In many regions of the world, top predators have been removed from the ecosystems by anthropogenic causes, resulting in profound changes to the abundance and organization of lower trophic levels [4]. With the loss of keystone predators, herbivorous prey can increase in size and abundance to the point where increased grazing rates can cause communities to switch from a state dominated by primary producers to one dominated by herbivores [5, 6]. These changes are exemplified on temperate rocky reefs, where the removal of keystone predators (e.g., sea otters) often causes a marked increase in herbivorous sea urchins, resulting in a shift from kelp forests to sea urchin

barrens [7, 8]. Sea urchin barrens have also become more common across kelp forest ecosystems worldwide due to food web modification and climate change [9–12]. Sea urchin barrens will generally persist until some episodic event or acute perturbation, such as disease [13], storm events [14], or removal via fisheries or predator recovery [15, 16], reduces sea urchin density and biomass [17].

In addition to the top-down effects of keystone predators, environmental forces can play a vital role in structuring sea urchin demographics by influencing their recruitment. Examples from Norway [18–21], the northeast Atlantic coast [22], Australia [23], the Gulf of Maine [15], and parts of the Aleutian Islands [24, 25] have shown variable effects of environmental drivers on patterns of sea urchin demography (Table 1). For instance, changes in sea surface temperature facilitated the range expansion of some high-latitude sea urchin populations [26]. Salinity, temperature, and current velocity influence early developmental phases of sea urchins, such as dispersal patterns and planktonic larval duration [22, 27, 28]. Habitat features such as exposure to incoming storms, slope of the seafloor, mean and variability of water depth, and spatial extent of deep or shallow water habitat could all influence sea urchin larval movement, survival, and their ability to recruit from deep water or complex refugia [29–31]. In oceanic island systems like the Aleutian archipelago, geophysical properties of island size, elevation, and steepness serve as proxy indices for potential inputs from land (e.g., freshwater runoff and nutrients) to the ocean [32, 33] and can also influence currents around islands. The aforementioned environmental factors are likely to influence the supply of recruits, ultimately maintaining sea urchin barrens, as well as adult sea urchin density and population size structure [18, 19, 34–36].

Although it is understood that sea urchin demographics may be influenced by their environment, the influence that the loss of a keystone predator has on environmental forcing of sea urchin demographics is largely unknown. The Aleutian archipelago serves as a model system that evaluates how sea urchin demographics are influenced by environmental forcing across a changing landscape of predator abundance. Sea otters were nearly driven to extinction in the 19th century by the Pacific maritime fur trade, which lasted until the Northern Fur Seal Treaty in 1911 [37]. By that time, less than a dozen remnant sea otter colonies remained. These colonies subsequently increased in abundance and distribution to repatriate much, but not all, of the Aleutian archipelago by the 1970s, allowing for comparisons among islands with and without sea otters [7, 38]. However, a precipitous decline in sea otter abundance occurred across the archipelago in the early 1990s, likely due to killer whale predation [39, 40]. By the early 2000s, sea otter abundance had been reduced by 90% at most islands [41]. This dramatic reduction in sea otter abundance propelled a rapid shift in the nearshore ecosystem, from kelp forests to sea urchin barrens, with associated changes in ecosystem structure and function [15, 42–45]. Sea otters remain functionally extinct throughout most of the archipelago [40, 46] and the benthic habitat around most Aleutian Islands remains in the urchin barren state [46]. A large-scale shift back to the kelp forest state appears likely to be contingent

on the recovery of sea otters; however, sea urchin demographics will probably continue to vary due to differences in local habitats [47].

In this study, we explore changes in the density, biomass, and size structure of sea urchin populations following the functional extinction of sea otters—their principal predator. We then link variation in sea urchin demography through space and time to environmental covariates. To do this, we used data obtained over 30 years from 15 Aleutian Islands to explore how sea urchin demography changed among periods when (1) sea otters were abundant and ecologically functional and benthic ecosystems were in a kelp-dominated state, (2) sea otters were in decline or recently declined and ecosystems were in transition to an sea urchin-dominated state, (3) a decade after sea otter populations had collapsed and the ecosystem was in a fully sea urchin-dominated state, and (4) 15-20 years after the ecological loss of sea otters, where the ecosystem remained in a barren state. We tested the hypotheses that sea urchin density, biomass, and proportion of large individuals would all increase in the absence of sea otter predation. We then explored which environmental factors best explained differences in sea urchin demography within and among the four aforementioned time periods.

2. Methods

2.1. Study Area and Site Selection. The Aleutian archipelago is a volcanic island chain spanning ~1900 km between the Alaska Peninsula, United States in the east, and the Kamchatka Peninsula, Russia, in the west and separates the Bering Sea from the North Pacific Ocean. Environmental gradients across the Aleutian archipelago are mirrored by clines in marine ecosystem dynamics [24, 48]. Variation in oceanographic properties such as temperature, salinity, current velocity, and bathymetry drives broad-scale patterns in pelagic marine community structure, with the oceanic passes that separate island groups creating boundaries between ecoregions [49]. The oceanic passes vary in depth, width, and total water volume transport (Figure 1; [48, 50–52]). Variation in nearshore benthic community structure is thus largely delineated by the identified biogeographic regions [24, 44].

We gathered data across this region to compile a 30-year dataset (1987-2017) from 235 distinct, randomly selected, permanent kelp forest monitoring sites distributed among the 15 islands (15-30 sites per island) (Figure 1 and Table 2; [8, 53]). These sites were initially selected from intersections using a grid superimposed over the island's perimeter and later through a GIS-based routine in ARC GIS to generate random point distributions along the 7 m depth contour (see [8] for details on site selection). While some variation occurred due to inclement weather and timing, attempts were made to survey at least six sites during each island-by-year resample (Table 2). Sites were initially marked and resurveyed using nautical charts, lineups, and institutional knowledge, until handheld GPS became available for navigation to specific coordinates using small boats. Only sites featuring rocky-bottom habitat capable of supporting kelps were selected, and those sites that were sand or gravel dominated were excluded from the sampling pool.

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TABLE 1: Examples of environmental variables that can influence sea urchin demographics in temperate urchin barrens.

Type of influence	Variable in this study	Scale in this study	Rationale	Expected influence +/-/?	Sources
	Sea surface salinity	Island	*Strongylocentrotus* spp. have a generally low tolerance to low and highly variable salinities	—	
Oceanographic	Sea surface temperature	Island	Temperature can influence the behaviour, reproduction, grazing, and growth of green sea urchins. Particularly important in large-scale climate studies	Mixed	[21, 22, 26, 28, 44, 46, 95]
	Sea surface current velocity	Island	Can influence patterns of sea urchin demographics by driving recruitment and local community structure	Mixed	
	Exposure	Site	Important local driver of sea urchin behaviour, size structure, and ecological function	Mixed	
	Slope	Site	Slope will shape patterns of sea urchin behaviour in response to perturbation across depth ranges	+	
	Slope variability	Site	Variability in slope can serve as a measure of complexity of local habitat, influencing sea urchin behavioural responses to perturbations across depth ranges	+	
	Depth	Site	Depth will shape patterns of sea urchin behaviour and ecological function	Mixed	
Bathymetric	Depth variability	Site	Variability in depth can serve as a measure of the complexity of the local habitat, influencing sea urchin behaviour and ecological function	+	[15, 18–21, 29–31, 38, 44, 95, 96]
	Shallow habitat	Site	The amount of shallow habitat within the foraging depths of sea otters and also in the ideal depth range for macroalgal production	+	
	Deep habitat	Site	The amount of deep water inaccessible to sea otters that could serve as a deep water refugia	+	
	Amount of shelf habitat	Site	The amount of habitat on the continental shelf (0-200 m water depth)	+	
Geophysical	Shape	Island	Can influence local currents, weather patterns, and degree of coastal *vs.* oceanic influence. Geophysical structure of the shoreline can influence other environmental forces	?	[27, 96]
	Mean elevation	Island		?	

Variables are listed by the type of influence. Rationale for inclusion was based on referenced sources with expected influence on urchin demographics: positive (+), negative (-), mixed, or unknown (?). This is not an exhaustive literature review and presents examples from temperate urchin barrens where sea otters are not a functional component of the ecosystem.
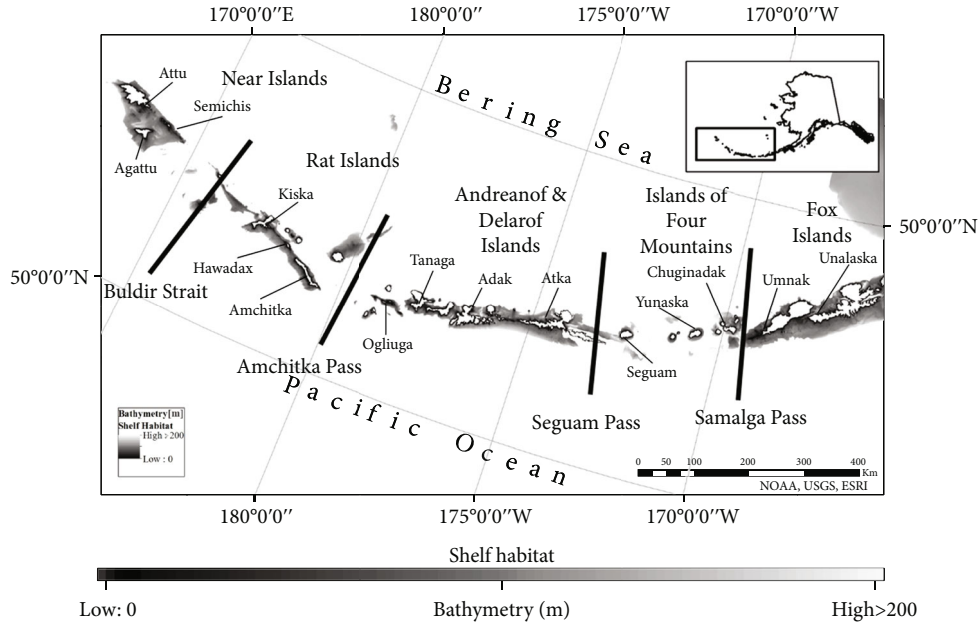
FIGURE 1: Map of the Aleutian archipelago with labels for study islands and major oceanic passes that separate island groups from west to east: Near Islands (Attu, Agattu, and Semichi Islands), Rat Islands (Kiska, Hawadax, and Amchitka), Delarof and Andreanof Islands (Ogliuga, Tanaga, Adak, and Atka), Islands of Four Mountains (Seguam, Yunaska, and Chuginadak), and Fox Islands (Umnak and Unalaska). Nearshore bathymetry (gray shading) shows continental shelf area, where depth ≤ 200 m [93].

TABLE 2: Number of sites sampled by island and year.

Island group	Island	Predecline				End of decline			Postdecline 1			Postdecline 2		
		1987	1990	1993	1994	1997	1999	2000	2008	2010	2014	2015	2016	2017
Near Islands	Attu	10	14	18	*2*	-	-	21	22	-	6	4	-	6
	Agattu	-	-	6	-	-	-	-	6	-	-	4	-	-
	Semichi	33	-	*1*	29	30	-	-	33	-	6	6	-	5
Rat Islands	Kiska	-	-	20	-	-	-	20	20	-	6	6	-	5
	Hawadax	-	-	-	13	-	-	-	15	*1*	-	6	-	-
	Amchitka	29	-	-	-	-	31	11	31	-	6	5	-	6
Andreanof and Delarof Islands	Ogliuga	-	-	-	4	-	-		10	-	6	6	-	6
	Tanaga	-	-	-	13	-	-	-	4	-	6	-	5	-
	Adak	28	-	-	-	27	30	29	30	-	6	4	6	6
	Atka	-	-	-	-	-	-	-	10	-	-	-	3	6
Islands of Four Mountains	Seguam	-	-	-	10	-	-	-	-	7	-	-	-	-
	Yunaska	-	-	-	12	-	-	-	-	-	-	-	-	6
	Chuginadak	-	-	-	12	-	-	-	12	-	-	-	6	-
Fox Islands	Umnak	-	-	-	8	-	-	-	-	-	-	-	6	-
	Unalaska	-	-	-	12	-	-	-	-	*2*	-	-	6	-

Italicized numbers (<4) denote samples excluded from analysis for inadequate sample size. Dashes correspond to no available data.

2.2. Sea Urchin Data. Density, biomass, population size structure, and recruitment of Aleutian green sea urchins (*Strongylocentrotus* spp.) were determined at each site for each given year of sampling. At each site, up to twenty $0.25\,m^2$ quadrats were haphazardly placed on the seafloor at least 3 m apart from one another and divers removed all sea urchins contained within each quadrat, or until at least 200 individuals were collected. A minimum of four quadrats were sampled even if 200 urchins were collected in the first quadrat in order to estimate spatial variability in density. Both green sea urchin species, *S. polyacanthus* and *S. droebachiensis*, can cooccur across the region and were treated as

Strongylocentrotus spp. for analyses because field determinations between *S. polyacanthus* and *S. droebachiensis* cannot be done and require genetic or laboratory work [54]. We note that it has been historically assumed that *S. polyacanthus* predominated the Aleutian archipelago with the size structure and functional role for the two species being similar across region [44]. Once aboard the ship or on land, the test diameter (i.e., the distance across the widest part of the sea urchin's outer skeleton excluding spines) was measured to the nearest millimeter using calipers. Size frequency data were truncated at a lower limit of 5 mm due to the mesh size of our collection bags. These data are accessible and archived in Ebert *et al.* [53] and with the Biological & Chemical Oceanography Data Management Office as epibenthic community abundance [55]. Sea urchin biomass density was calculated using a published size (test diameter (TD)) to wet mass (grams) relationship ($-7.857 + (2.992^{*}Log[TD])$) for green sea urchins from the Aleutians [56].

2.3. Environmental Data Acquisition.
Environmental variables (Table 1) were quantified at site or island scales, depending on the resolution of the available data. Site-level data were derived using the latitude and longitude of each site, while island-level data were derived from a calculated centroid among sites at each island. Centroids were calculated in GIS (ArcMap10.3, ESRI) as the mean distance among site coordinates by each island. Oceanographic data were obtained from publicly available datasets hosted by the Alaska Ocean Observing System (https://portal.aoos.org/#module-metadata/4f706756-7d57-11e3-bce5-00219bfe5678) using their virtual sensor tool with modelled climate data for the southern Bering Sea to extract values of surface ocean temperature, salinity, and current velocity for each island. The oceanographic data resolution was at 5 km cells, so a value for each metric was extracted from the cell containing the island's centroid position. The oceanographic data were modelled for the entire water column, from 2002 to 2040, by the Pacific Marine Environmental Laboratory and the Canadian Centre for Climate Modelling and Analysis [57] to support modelling of oceanographic changes throughout the Bering Sea [58]. We averaged annual means from the three most comprehensive open-access models found for this area for the upper 20 m of the water column for ocean temperature, salinity, and current velocity to characterize the mean and variance for these attributes at each island.

Bathymetric variables were quantified for each sampling site by creating a 1 km buffer ring (0.5 km radius) around each site's geographic position and clipping segments of coastline and bathymetry raster to the boundaries of the site buffer. Bathymetry data were obtained from the National Oceanic and Atmospheric Administration [59] and processed in ArcMap10.6, from a raster grid file at 20 m resolution. Within each site buffer ring, a mean and variance of depth and bathymetric slope were calculated among all raster cells below the 0 m isobath. The total area of cells contained within each buffer ring was calculated to represent the area of seafloor around a site, serving as a coarse proxy for potential exposure where land features would reduce the total area from the maximum of 0.79 km² (area of 1 km buffer with no land). The size of the coastal shelf around

each site was calculated as the area within each buffer ring between the 0 and 200 m isobaths. Total area of shallow habitat (<60 m depth) and deep habitat (>60 m depth) was also calculated within each buffer ring.

Geophysical attributes of each island were calculated using vector data from U.S. Geological Survey topographic and coastline segments for the Aleutians in ArcMap10.6 and applying the spatial analyst geometry toolkit. Island size and shape were determined by measuring the perimeter (kilometer) and area (hectare) of each island and then calculating a perimeter/area ratio. Island elevation was determined by calculating the maximum and mean elevation (meter) for each island. Island thickness was calculated as another measure of island shape, where thickness represents the greatest distance from the edge to center of an island's land mass. Island steepness was calculated as the mean slope of land for each island.

2.4. Spatiotemporal Analysis of Sea Urchin Demography.
For spatial analyses, we examined islands and island regions at their grouped scales (Table 2), where sampling areas and islands in close proximity were combined (i.e., the Semichi Islands were comprised of Shemya, Alaid, and Nizki Islands; Attu Island included Massacre Bay and Pisa Point; Tanaga Island included Hot Springs Bay and Tanaga Bay; Ogliuga Island included adjacent Skagul Island; and Umnak Island included adjacent Anangula Island). To examine changes in sea urchin demographics over the sea otter decline, four time periods representing different ecosystem states were identified between 1987 and 2017. Specifically, these were (1) predecline (1987-1994), when sea otters were present and relatively abundant (although there was some variability in abundance among islands caused by differences in timing of sea otter recovery postfur trade; [40]) and most islands were predominantly in a kelp forest state; (2) end of decline (1997-2000), when sea otters were largely absent from the system and most islands were in a state of transition; and (3 and 4) two time periods after the decline occurred (postdecline 1, 2008-2010, and postdecline 2, 2014-2017), when sea otters were functionally extinct from the system and islands were predominantly in the urchin barren state. The latter two time periods, which represent roughly a decade postdecline and then 15-20 years postdecline, were used to gauge longer-term changes to sea urchin demography in the absence of sea otters. We limited our analyses to island-year combinations with at least four sites sampled during each year in question (Table 2). Changes in sea urchin abundance and biomass among the four time periods and 15 islands were analyzed in Primer-e v7 [60] using separate univariate two-way, fixed-factor permutational analyses of variance (PERMANOVA, [61]), with the resemblance matrix based on Euclidean distances because the data were continuous and contained many meaningful zeroes. Following each PERMANOVA, the percent contribution of each factor to the model's total variability was determined by calculating their magnitude of effects (ω^2) using variance component analyses as described by Graham and Edwards [62].

Green sea urchin size frequency distributions were determined by first summing the number of individuals collected

from each site within discrete 1 mm size class bins. The counts in each bin were then averaged across the different sites at each island to provide an estimate for each island-year survey combination. Each of the 1 mm size class bins was treated as an ordered variable within a multivariate analysis of the complete size structure. Data were standardized, and a Manhattan distance-based resemblance matrix was constructed with no transformation to preserve the frequency distributions [63] and so that individual size classes could be examined in relation to the environment and by space and time. To evaluate differences in size frequencies among the four time periods and 15 islands, a two-way fixed-factor PERMANOVA was performed on the resemblance matrix, with permutations done under a reduced model. This was again followed by calculating each factor's magnitude of effects. The 1 mm binned size data were also used to construct line plots and metric multidimensional scaling (mMDS) ordinations for visualizing patterns in sea urchin size distributions among island-period samples.

Size frequency data were next collapsed into broader size categories to determine the general size of sea urchins driving differences in frequency distributions within each time period. Here, size categories were defined as recruit (≤20 mm), small (21-35 mm), medium (36-55 mm), large (56-65 mm), and extralarge (66-100 mm). These categories were determined based on the size-selective preferences by sea otters for predating medium and larger sea urchins [44] and the likelihood that sea urchins < 20 mm in test diameter were less than 2 years old and unlikely to have reached sexual maturity [64, 65]. To determine the relative contribution of each size category to differences in size distributions among time periods, a similarity percentage analysis (SIMPER) was performed on the categorized data. A recruitment index was then calculated based on the proportion of sea urchin recruits in each island-time period sample. For the following tests of recruits, three of the islands were excluded from analyses due to no predecline data (Atka) or limited sample sizes (Umnak and Unalaska). A Euclidean distance-based resemblance matrix was constructed on the resulting proportional data, and a two-way fixed-factor univariate PERMANOVA was performed on the resemblance matrix using unrestricted permutations. This again was followed by calculating each factor's magnitude of effects. Bubble plots were overlaid on the mMDS of sea urchin size frequency distributions to show differences in the recruitment index among island-period combinations.

2.5. Correlations of Environmental Data with Sea Urchin Size Distributions. Correlations of environmental variables with sea urchin size distributions were determined using the Bio-Env (BEST) procedure in Primer v7 [61]. Environmental variables were compared using draftsman plots to identify correlations among predictor variables and determine necessary transformations. Island area, perimeter length, variability of slope, and island mean and max elevation were excluded due to autocorrelation exceeding 0.8 with other variables, leading to the selection of the following 11 environmental

variables: temperature, salinity, current velocity, exposure, deep habitat area, shallow habitat area, bathymetric slope, depth variability, island size (perimeter : area), island steepness, and island thickness. Prior to the BEST analysis, variables of island size, steepness, depth variability, and deep habitat area were log transformed, salinity was exponentially transformed, and all other variables were untransformed. Then, all variables were centered and scaled to unit variance [60, 63]. The BEST routine was performed on the standardized and cumulated Manhattan distance matrix of sea urchin size structure, generated as described above. Each time period of sea otter status was analyzed independently, predecline, end of decline, postdecline 1, and postdecline 2, with a permutation test to produce a significance value and ρ (rho) statistic for comparison of BEST fit among analyses. The BEST variable selection procedure was used to determine which variables were most correlated with patterns of sea urchin size structure, when only a limited number of variables were used, beginning with a single variable and increasing to six variables. Correlation values for the ten best-fit multiple environmental variable models were compared by the spearman rank correlation value. Principal component analysis was used to describe the differences in environmental variables among islands.

3. Results

Sea urchin densities varied significantly among time periods (PERMANOVA: $pseudo - F_{3,757} = 3.389$, $p(\text{perm}) = 0.018$) and islands ($pseudo - F_{15,757} = 32.637$, $p(\text{perm}) = 0.001$), but the trends among time periods were not consistent across the different islands (time period×island interaction: $pseudo - F_{28,757} = 8.721$, $p(\text{perm}) = 0.001$) (Table 3 (a)). Variation among islands explained over 34% of the total variability in sea urchin density while variation among time periods explained less than 1% of the total variability, and variation due to the time period×island interaction explained a little over 21% of the total variability (Table 3(a)). Specifically, while sea urchin densities varied among periods of predecline to end of decline, postdecline 1, and postdecline 2 at Attu, Agattu, Semichi Islands, Kiska, Amchitka, and Seguam (pairwise tests: $p(\text{perm}) < 0.05$), densities at Ogliuga, Tanaga, Yunaska, Umnak, and Unalaska were not significantly different among time periods (Figure 2). Further, sea urchin densities at Adak were significantly different between predecline and postdecline 1, but no significant differences were observed between predecline and postdecline 2. No significant differences were observed between postdecline 1 and postdecline 2 periods for any of the islands, including Atka (which was not sampled predecline), indicating that despite observed variability, densities were generally similar following the long-term absence of sea otters (Figure 2). Overall, sea urchin densities experienced their greatest degree of change immediately following loss of predatory control by sea otters, and then, they remained at higher densities.

Sea urchin biomass also varied significantly among time periods (PERMANOVA: $pseudo - F_{3,757} = 10.697$, $p(\text{perm})$

TABLE 3: PERMANOVA results for the main tests of sea urchin density, biomass, size distributions, and recruitment index.

(a) Density

Source	SOS	df	MS	Pseudo-F	p(perm)	ω^2
Island	$5.98E + 05$	14	39892	32.637	0.001	0.344
Period	12426	3	4142	3.389	0.018	0.009
Island×period	$2.98E + 05$	28	10660	8.721	0.001	0.213
Residual	$9.25E + 05$	757	1222.3			0.434

(b) Biomass

SOS	df	MS	Pseudo-F	p(perm)	ω^2
$1.21E + 07$	14	$8.05E + 05$	7.943	0.001	0.118
$3.25E + 06$	3	$1.08E + 06$	10.697	0.001	0.057
$1.23E + 07$	28	$4.41E + 05$	4.350	0.001	0.145
$7.67E + 07$	757	$1.01E + 05$			0.680

(c) Size distribution

Source	SOS	df	MS	Pseudo-F	p(perm)	ω^2
Island	$6.28E + 08$	14	$4.49E + 07$	61.519	0.001	0.375
Period	$1.22E + 08$	3	$4.07E + 07$	55.700	0.001	0.113
Island×period	$3.03E + 08$	30	$1.01E + 07$	13.837	0.001	0.224
Residual	$5.90E + 08$	808	$7.30E + 05$			0.288

(d) Recruitment index

SOS	df	MS	Pseudo-F	p(perm)	ω^2
28.157	11	2.56	51.716	0.001	0.367
6.175	3	2.058	41.586	0.001	0.120
8.662	25	0.347	7.001	0.001	0.127
37.321	754	0.049			0.386

= 0.001) and islands (pseudo $- F_{15,757} = 7.943$, p(perm) = 0.001), but the trends among time periods were again not consistent across the different islands (time period×island interaction: pseudo $- F_{28,757} = 4.350$, p(perm) = 0.001) (Table 3(b)). Variation among islands explained a little under 12% of the total variability in sea urchin biomass while variation among time periods explained just under 6% of the total variability, and variation due to the time period×island interaction explained over 14% of the total variability (Table 3(b)). In particular, while sea urchin biomass varied among periods of predecline to end of decline, postdecline 1, and postdecline 2 at Attu, Agattu, Kiska, Amchitka, Ogliuga, Tanaga, Adak, Seguam, and Unalaska (pairwise tests: p(perm) < 0.05), biomass at Semichi Islands, Hawadax, Yunaska, Chuginadak, and Umnak was not significantly different among periods (Figure 2). No significant differences were observed between postdecline 1 and postdecline 2 periods for any of the islands, including Atka (which was not sampled predecline).

As with both density and biomass, sea urchin size frequency distributions varied significantly among time periods (PERMANOVA: pseudo $- F_{3,808} = 55.700$, p(perm) = 0.001) and islands (pseudo $- F_{15,808} = 61.519$, p(perm) = 0.001), but the trends through time again were not consistent across the different islands (time period×island interaction: pseudo $- F_{30,808} = 13,837$, p(perm) = 0.001). Variation among islands explained over 37% of the total variability in sea urchin size frequencies while variation among time periods explained just over 11% of the total variability, and variation due to the time period×island interaction explained a little over 22% of the total variability (Table 3(c)). Specifically, sea urchin size frequencies varied significantly across time periods at Attu, Agattu, Semichi Islands Kiska, Ogliuga, Tanaga, Adak, and Seguam (pairwise tests: p(perm) < 0.05); however, the nature of change was quite different among those islands, particularly among island groups (Figure 3). Further, size frequencies at Amchitka were significantly different between predecline

(a)

(b)
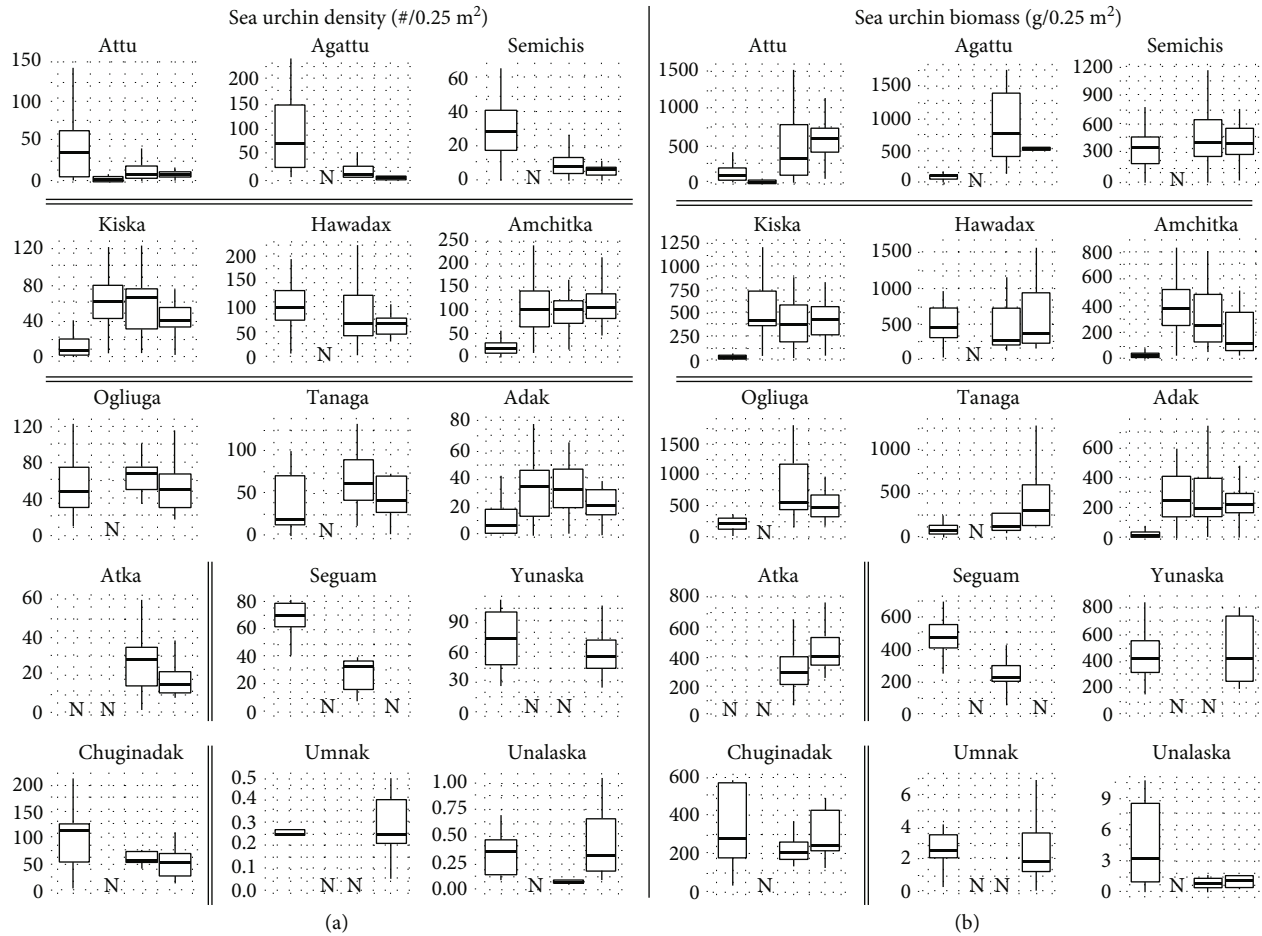
Sea otters: pre decline, end of decline, post decline 1, post decline 2

FIGURE 2: Boxplots of sea urchin density (a) and biomass (b) per 0.25 m², averaged by island (each facet) for each time period of sea otter status: predecline, end of decline, postdecline 1, and postdecline 2. N indicates no data. Barred lines denote passes that separate the island groups shown in Figure 1.

and end of decline, but then between pre- and postdecline periods, the difference was marginal. Similarly, Yunaska, Umnak, and Unalaska were significantly differently between predecline and postdecline 1, but not between predecline and postdecline 2. Size frequencies did differ between postdecline 1 and postdecline 2 at Hawadax, Chuginadak, Umnak, and Unalaska (Figure 3). Together, these findings revealed differing spatial patterns among islands during each time period (Table 3(c)).

Examination of the size classes that underpinned sea urchin size frequencies revealed that recruits (<20 mm) and small sea urchins (21–35 mm) together explained ≥66% of the differences in size distributions among all time periods (SIMPER: Table 4). Indeed, recruits and small sea urchins dominated populations at all islands during the predecline period (Figure 3). However, this pattern shifted in the end of decline period at Attu and the Semichi Islands, where small and medium (36–55 mm) urchins came to dominate, while recruits and small urchins continued to dominate at Kiska, Amchitka, and Adak (note: Agattu, Hawadax, Ogliuga, Tanaga, Atka, Seguam, Yunaska, Chuginadak, Umnak, and Unalaska were not sampled in the end

of decline period). Differences among islands continued into the postdecline 1 period, where recruits and small sea urchins continued to dominate at Kiska, Hawadax, Amchitka, Ogliuga, Tanaga, Adak, Atka, Seguam, Yunaska, and Chuginadak (though a second mode of larger urchins appeared during postdecline 1 at Hawadax and Chuginadak). The mode shifted entirely towards larger-bodied individuals as Attu, Agattu, and the Semichi Islands became dominated by medium and large (56–65 mm) sea urchins. East of Samalga Pass, Umnak, and Unalaska showed a change in the postdecline 1 period, where Umnak became dominated by medium and extralarge (66–100 mm) sea urchins, and Unalaska became dominated by small and medium sea urchins. By the postdecline 2 period, recruits and small sea urchins still dominated at Kiska, Hawadax, Amchitka, Ogliuga, Tanaga, Adak, Yunaska, Chuginadak, and Unalaska, while Atka and Umnak became dominated by small and medium sea urchins, and Attu, Agattu, and the Semichi Islands were dominated by large and extralarge sea urchins (Figure 3). Thus, the Near Islands (Attu, Agattu, and Semichi Islands)—where sea otters were still recovering from the fur trade prior to their recent system-wide
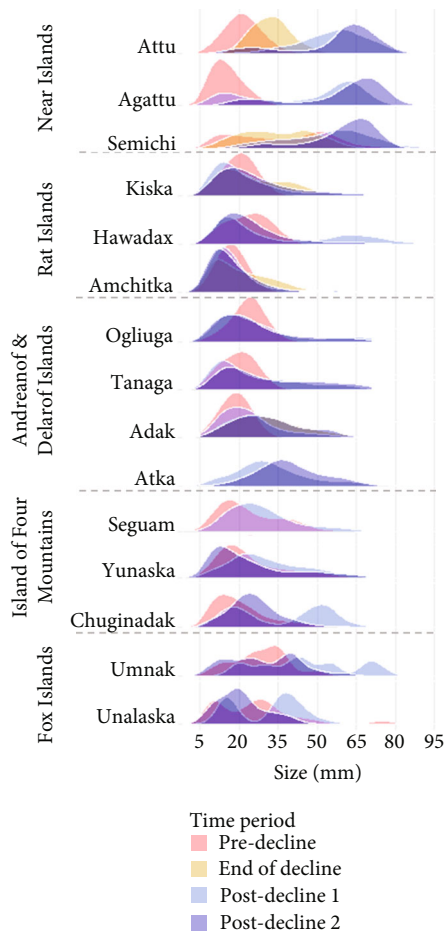
FIGURE 3: Proportional sea urchin size frequency distributions with sizes averaged by island (from west to east) and time period of sea otter status. *y*-axis for each plot is from 0 to 100%. No data available to show for predecline: Atka; end of decline: Hawadax, Ogliuga, Tanaga, Atka, Seguam, Yunaska, Chuginadak, Umnak, and Unalaska; and postdecline 2: Seguam. Horizontal dashed lines denote major passes that separate island groups.

collapse—became dominated by large sea urchins. Conversely, at islands where sea otters had recovered prior to their recent decline, large sea urchins did not come to dominate the population size structure.

Sea urchin recruitment, as determined by the proportion of small urchins at each site, was found to significantly vary among time periods (PERMANOVA: $\text{pseudo} - F_{3,754} = 41.586$, $p(\text{perm}) = 0.001$) and islands ($\text{pseudo} - F_{11,754} = 51.716$, $p(\text{perm}) = 0.001$), with trends not being consistent among islands through time (time period×island interaction: $\text{pseudo} - F_{25,754} = 7.001$, $p(\text{perm}) = 0.001$) (Table 3(d)). Variation among islands explained over 36% of the total variability in sea urchin size frequencies while variation among time periods explained 12% of the total variability, and variation due to the time period×island interaction explained a little under 13% of the total variability (Table 3(d)). Specifically, in the predecline period, Attu, Agattu, Semichi Islands, Adak, Seguam, and Yunaska had significantly higher recruitment indices than in postdecline periods (Figure 4). At Kiska, Amchitka, Tanaga, and Chugina-

dak, recruitment decreased between pre- and postdecline only slightly (Figure 4). Hawadax and Ogliuga showed slight increases between pre- and postdecline, while Umnak and Unalaska were not analyzed due to low sample size in the Fox Islands but did not appear to change. Amchitka consistently had a significantly higher recruitment rate than all other islands in both pre- and postdecline periods. Generally, in the postdecline periods, the Near Island group (Attu, Agattu, and the Semichi Islands) had lower recruitment than other islands in the western and central Aleutians, despite Agattu having some of the highest recruitment in predecline, while the eastern Fox Islands had few sea urchin recruits. Recruitment was higher when sea otters were present in the system and decreased at most islands during postdecline periods (Figure 4). Islands that had more variable and lower recruitment exhibited greater variability in size distributions over time (Attu, Semichi Islands, and Agattu), whereas islands with higher or more stable levels of recruitment exhibited greater similarity in population size structure over time (e.g., Amchitka) (Figure 5). The Near Islands (Attu, Agattu, and Semichi Islands) exhibited the largest change in sea urchin size over time, primarily because of little to no recruitment of small sea urchins. In contrast, the trajectory for the Islands of Four Mountains group (Seguam, Yunaska, and Chuginadak) differed from the Andreanof and Delarof (Ogliuga, Tanaga, and Adak) and Rat (Kiska, Hawadax, and Amchitka) island groups in that size frequencies were more similar over time periods of sea otter decline (Figure 5).

The environmental variables were at first weakly correlated with sea urchin size structure, but correlations grew stronger as time progressed (Table 5). In the predecline period, a combination of three environmental variables—namely, island size (perimeter : area), exposure, and temperature—best predicted sea urchin size frequency distributions, yet these variables showed only a weak but significant correlation with size structure ($\rho = 0.329$, $p = 0.001$). The single variable most correlated with sea urchin size frequency distribution during this period was island size ($\rho = 0.260$). In the end of decline period, a combination of four variables—namely, island size, steepness, exposure, and deep habitat area—best predicted sea urchin size frequency distributions, but these again showed an even weaker (though still significant) correlation with size distribution ($\rho = 0.155$, $p = 0.001$). The variable most correlated with urchin size structure was again island size ($\rho = 0.152$); however, its correlation value was the same as those observed for the best two variables—island size and salinity—and for the best three variables: island size, exposure, and current velocity. These correlations increased in strength again during the postdecline 1 period, when two variables—namely, island size and seawater temperature—were most correlated with sea urchin size frequency distributions ($\rho = 0.375$, $p = 0.001$). During this period, the single most correlated variable was temperature ($\rho = 0.354$). These correlations increased in strength yet again in the postdecline 2 period, when temperature alone exhibited the best correlation with size frequency distribution ($\rho = 0.403$, $p = 0.001$). Thus, during the two postdecline periods, the strongest correlations involved some combination of temperature, island size, and/or exposure

TABLE 4: SIMPER analyses comparing the relative contribution of each of the five binned size classes to the observed differences among time periods.

Predecline vs. end of decline
Average dissimilarity = 57.21

Size Category	Predecline Av.Abund	End of decline Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Recruit	87.43	80.38	26.14	1.21	45.69	45.69
Small	43.13	70.15	18.72	1.17	32.71	78.41
Medium	12.34	34.51	10.84	0.89	18.95	97.35
Large	1.87	1.89	1.13	0.43	1.97	99.32
Extralarge	0.94	0.2	0.39	0.18	0.68	100

Predecline vs. postdecline 1
Average dissimilarity = 58.47

Species	Predecline Av.Abund	Postdecline 1 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Recruit	87.43	89.92	26.36	1.28	45.09	45.09
Small	43.13	44.59	14.16	1.1	24.21	69.3
Medium	12.34	31.05	10.28	0.84	17.59	86.89
Large	1.87	14.44	5.15	0.62	8.81	95.7
Extralarge	0.94	6.4	2.51	0.39	4.3	100

End of decline vs. postdecline 1
Average dissimilarity = 58.46

Species	End of decline Av.Abund	Postdecline 1 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Recruit	80.38	89.92	24.57	1.17	42.03	42.03
Small	70.15	44.59	15.99	1.16	27.36	69.39
Medium	34.51	31.05	11.24	0.93	19.22	88.61
Large	1.89	14.44	4.54	0.6	7.77	96.39
Extralarge	0.2	6.4	2.11	0.36	3.61	100

Predecline vs. postdecline 2
Average dissimilarity = 60.40

Species	Predecline Av.Abund	Postdecline 2 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Recruit	87.43	97.13	26.37	1.3	43.66	43.66
Small	43.13	55.84	15.17	1.1	25.12	68.78
Medium	12.34	27.65	8.71	0.81	14.42	83.2
Large	1.87	16.16	5.91	0.64	9.79	93
Extralarge	0.94	10.57	4.23	0.49	7	100

End of decline vs. postdecline 2
Average dissimilarity = 59.37

Species	End of decline Av.Abund	Postdecline 2 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Recruit	80.38	97.13	24.28	1.19	40.89	40.89
Small	70.15	55.84	16.08	1.12	27.09	67.97
Medium	34.51	27.65	10.14	0.89	17.08	85.06
Large	1.89	16.16	5.22	0.61	8.78	93.84
Extralarge	0.2	10.57	3.66	0.46	6.16	100

TABLE 4: Continued.

Postdecline 1 vs. postdecline 2
Average dissimilarity = 58.12

Species	Postdecline 1 Av.Abund	Postdecline 2 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Recruit	89.92	97.13	24.87	1.22	42.79	42.79
Small	44.59	55.84	13.48	1.09	23.19	65.98
Medium	31.05	27.65	9.45	0.88	16.25	82.23
Large	14.44	16.16	6.12	0.8	10.54	92.77
Extralarge	6.4	10.57	4.2	0.57	7.23	100
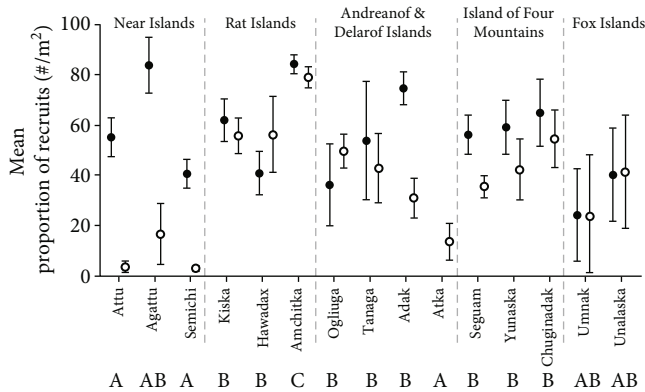
FIGURE 4: Sea urchin recruitment index means by island from west to east, with (closed) and without (open) sea otters. Points represent the predecline period and mean of the two postdecline (open) periods, and end of decline period is not shown. Error bars show standard deviation. Letters a, ab, b, and c denote pairwise significant among islands by PERMANOVA (p(perm) < 0.05) during postdecline periods. Dashed lines denote island groups. No data for Atka predecline period.

(Table 5). The strongest spatial environmental gradients observed across the archipelago were temperature and salinity (Figure 6); however, when all physical factors were considered together, islands within a group (i.e., Near, Rat, Delarof/ Andreanof, Island of Four Mountains, and Fox Islands) did not group together according to their environmental conditions (Figure 7). Rather, these island groupings appeared more strongly influenced by differences in static physical parameters that describe island shape and size (e.g., area, perimeter, and thickness) or bathymetry (e.g., depth, slope, and variability) among the islands and island groups (Figure 7).

4. Discussion

Our study explored patterns of variation in sea urchin density, biomass, and size structure in a rocky reef ecosystem where green sea urchin populations were historically controlled by sea otter predation. Our results confirm that the loss of keystone predation by sea otters led to greater variability in sea urchin population size structure and that environmental drivers like island size became more important in controlling sea urchin demography in the wake of the sea

otter population collapse. While correlations with environmental variables were generally weak throughout our multi-decadal study period, a pattern of environmental influence increasing following the loss of sea otters was revealed. It is likely, therefore, that the role of environmental forcing became more important over time in shaping patterns of sea urchin demography at the island and island group scales measured in this study following the functional loss of sea otters from the ecosystem.

Keystone species can cause profound changes to ecosystem structure and function via feeding on their prey [2], though susceptibility of an ecosystem to top-down control may be influenced by several environmental factors [3, 66]. Because variation in abiotic factors is always present, these factors have the ability to feed back through the food web and affect the strength and influence of species interactions [67]. In systems characterized by strong top-down interactions, responses to the addition or removal of a top predator can elicit variable ecosystem responses [9], depending in part on the strength of bottom-up forcing [68]. In the Aleutian archipelago, sea urchin demographics were similar among islands when they were under top-down control (i.e., when sea otters were present) and were generally characterized by small-sized sea urchins in modest abundances with an absence of large-sized sea urchins. However, following the functional extinction of sea otters, variability in sea urchin demographics increased across space and time as sea urchin recruitment and environmental forcing became more important. Our interpretation of this switch is that, when present in the system, sea otters effectively mask the roles of local-scale environmental forcing and sea urchin recruitment. This masking of environmental effects by predators has been observed in other ecosystems, where environmental forcing became more obvious and more important when top-down control was relaxed [42, 69, 70]. While environmental forcing appears to have become more influential on sea urchin demographics following the loss of predatory sea otters, the correlations we observed were still quite weak, suggesting that we may not have identified the full array of abiotic (and potentially biological) drivers operating in this system and/or that we did not measure each driver at its appropriate scale (e.g., using modelled dynamic variables for environmental metrics like temperature). Indeed, some environmental drivers act on ecosystems such as kelp forests most strongly at specific spatial scales [71], which can then
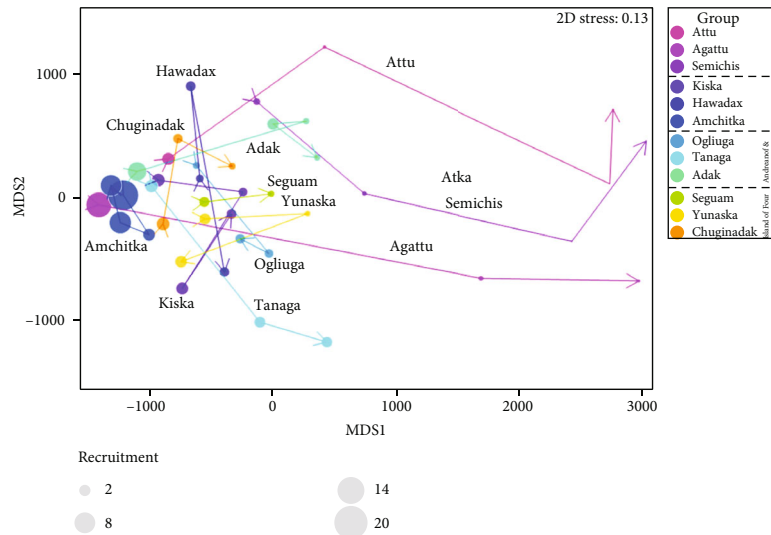
FIGURE 5: Metric MDS plot of sea urchin size distribution by island and time period of sea otter status. Bubble size depicts the average recruitment index (proportion of sea urchins $\leq 20\,\text{mm}$ per $0.25\,\text{m}^{-2}$) for each island period. Arrows sequentially connect the periods from predecline to end of decline to postdecline 1 to postdecline 2, except where only 3 points are connected and end of decline data were not available. Some islands were excluded due to no predecline data (Atka) or limited sample size (Umnak and Unalaska).

alter their spatial structuring at that scale [42]. These results were not surprising as sea urchins are renowned for their stochastic boom-bust population fluctuations and overall variability [72].

Spatial asynchrony in the recovery of sea otters across the Aleutian archipelago prior to the onset of their decline in the 1990's likely contributed to the variable responses of sea urchin demographics among study periods [41, 46, 73]. The Islands of Four Mountains island group were somewhat anomalous in that they displayed no significant change in sea urchin demographics across time periods; however, these steep volcanic islands experienced limited or no sea otter recovery (prior to the decline) due to a dearth of shallow water habitat [41]. In contrast, sea urchin size frequency distributions in the Near, Rat, Andreanof, and Delarof island groups, which have considerable shallow water habitat, were similar when sea otters were present but then diverged during periods of sea otter decline and absence.

Differences in sea urchin demographics between the Near Islands and other island groups in later years of sea otter absence (postdecline 2) appear to reflect differences in the rate of sea urchin recruitment (Figure 5). The Near Islands exhibited the largest change in sea urchin size structure in the wake of sea otter decline, compared to other island groups. This is primarily due to an increase in large sea urchins and little to no recruitment of small urchins after the decline. Sea otter populations in the Near Islands and Islands of Four Mountains had just begun to recover in the 1970s from the maritime fur trade, only to collapse again in the 1990s. This recovery trajectory differed from other island groups (i.e., Andreanof, Delarof, and Rat Islands) where sea otters were thought to have recovered to near carrying capacity by the 1950s [40, 41, 74]. Sea otters preferentially feed on large sea urchins (>45 mm), which may explain why large sea urchins were more abundant in the Near

Islands where sea otters had not recovered to near carrying capacity prior to the 1990s. At the Islands of Four Mountains where the continental shelf is quite narrow, it is probable that large sea urchins may have a depth refuge beyond the foraging range of sea otters (~100 m; [75]). Differences in sea otter population status at the start of this study may therefore help to explain the preponderance of large sea urchins in the Near Islands relative to other island groups but do not explain why there are so few large urchins elsewhere, nor why there are so few small individuals in the Near Islands. It is likely that recruitment, or rather a lack thereof, plays an important role in shaping patterns of sea urchin demographics among western Aleutian Islands.

Regardless of time period, sea urchin demographics differed markedly across Samalga Pass, which separates the Fox Islands from islands in the central and western ecoregions [49] and corresponds to a major biogeographic boundary in kelp forest communities [24]. Sea urchin barrens were virtually nonexistent to the east of Samalga Pass, while barrens were predominant to the west of Samalga Pass [24]. Top-down control by sea otters prior to the decline was quite apparent to the west of Samalga Pass, but their influence was less apparent in the Fox Islands or in the adjacent Islands of Four Mountains during that same period. Differing oceanographic characteristics between the Alaska Coastal Current, which floods the eastern islands in warmer, fresher, more coastally influenced water, and the Alaska Stream, which flows through the western side of Samalga Pass with colder, saltier, more oceanic water [48], may impact sea urchin life histories, with spillover effects on islands adjacent to and downstream of Samalga Pass. The temperature and salinity gradients across the Aleutians appear to reflect these regional oceanographic patterns (Figure 6). Most of the sampling for this study took place to the west of Samalga Pass, and variability in salinity was

TABLE 5: Correlation values from BEST analysis of environmental variable with sea urchin size distributions. Among all islands in each time period of sea otter status, the number of variables (# vars.), Pearson correlation value (corr.), and variables included (variables) in the best correlation combinations are shown. Strength of correlation statistic (ρ value) and significance of test by permutations (perms = 999) separate the results for best correlations with a limited variable set and best correlations by combination variable set.

	Correlations with Sea Urchin Size Distributions by Time Period of Sea Otter Status											
Sea otter period	Predecline			End of decline			Postdecline 1			Postdecline 2		
	# vars.	Corr.	Variables	# vars.	Corr.	Variables	# vars.	Corr.	Variables	# vars.	Corr.	Variables
Number of Variables, Correlations, Variables included	1	0.260	1	1	0.152	1	1	0.354	10	1	0.403	10
	2	0.318	1, 4	2	0.152	1, 9	2	0.375	1, 10	2	0.371	4, 10
	3	0.329	1, 4, 10	3	0.152	1, 4, 11	3	0.352	1, 4, 10	3	0.328	1, 4, 10
	4	0.327	1, 2, 4, 10	4	0.155	1, 3, 4, 8	4	0.312	1, 4, 10, 11	4	0.287	1, 4, 8, 10
	5	0.321	1, 2, 4, 9, 10	5	0.150	1, 3, 4, 8, 11	5	0.267	1, 4, 8, 10, 11	5	0.236	1, 4, 8, 10, 11
	6	0.298	1, 2, 4, 7, 9, 10	6	0.151	1, 3, 4, 8, 10, 11	6	0.220	1, 4, 8-11	6	0.192	1, 2, 4, 8-10
ρ value (best corr.)		0.329			0.155			0.375			0.403	
Sig. of sample stat.		0.1%			0.1%			0.1%			0.1%	
10 best variable combinations: number of variables, correlations, variables included	3	0.329	1, 4, 10	4	0.155	1, 3, 4, 8	2	0.375	1, 10	1	0.403	10
	4	0.327	1, 2, 4, 10	1	0.152	1	1	0.354	10	2	0.371	4, 10
	3	0.326	1, 4, 9	2	0.152	1, 9	3	0.352	1, 4, 10	3	0.328	1, 4, 10
	4	0.323	1, 2, 4, 9	3	0.152	1, 4, 11	2	0.321	4, 10	2	0.321	1, 10
	4	0.322	1, 4, 9, 10	4	0.152	1, 4, 9, 11	4	0.312	1, 4, 10, 11	3	0.310	4, 8, 10
	5	0.321	1, 2, 4, 9, 10	6	0.151	1, 3, 4, 8, 10, 11	1	0.309	1	3	0.296	4, 10, 11
	2	0.318	1, 4	3	0.151	1, 4, 8	3	0.305	1, 10, 11	2	0.294	8, 10
	3	0.317	1, 2, 4	4	0.151	1, 4, 8, 9	2	0.296	10, 11	2	0.289	10, 11
	4	0.313	1, 3, 4, 10	2	0.151	4, 11	2	0.291	1, 4	4	0.287	1, 4, 8, 10
	5	0.308	1-4, 10	2	0.150	1, 4	3	0.288	1, 8, 10	3	0.281	4, 9, 10

Codes for "variables" are as follows: (1) island size, (2) island thickness, (3) island steepness, (4) exposure (site area), (5) bathymetric slope, (6) depth variability, (7) shallow habitat area, (8) deep habitat area, (9) salinity, (10) temperature, and (11) current velocity.
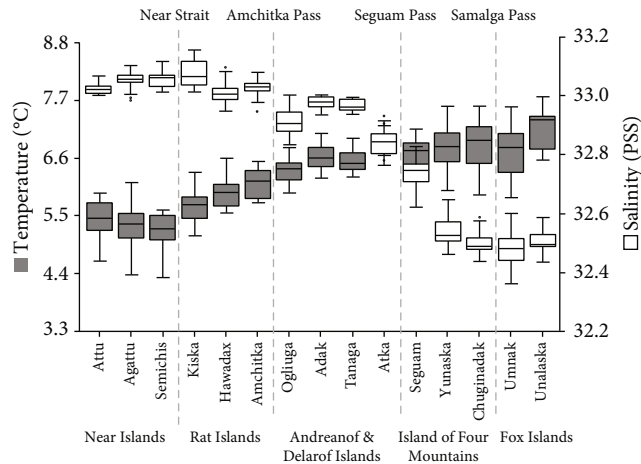
FIGURE 6: Box plot of mean sea surface temperature (gray) and salinity (white) across the upper 20 m of the water column, averaged from PMEL CCMA model [94] across years 2002-2017 by island from west to east. Dashed lines denote major passes that separate island groups.
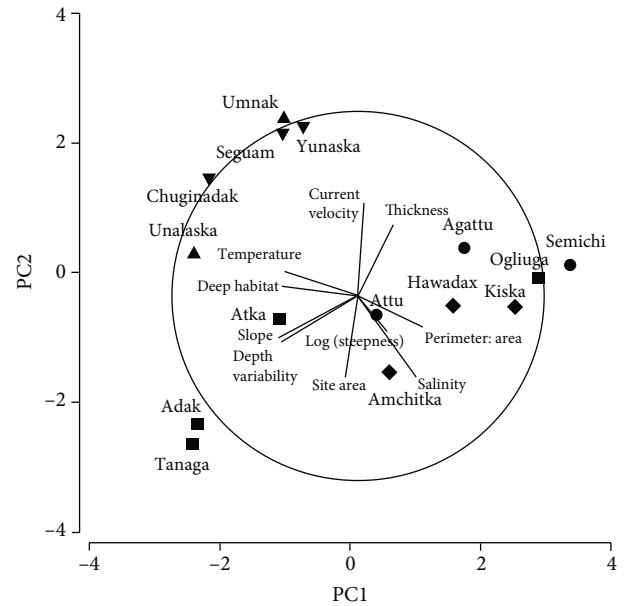

FIGURE 7: Principal component analysis (PCA) of environmental variables, coded by island group: Near Islands (circles), Rat Islands (diamonds), Delarof and Andreanof Islands (squares), Island of Four Mountains (down triangles), and Fox Islands (up triangles). The vectors depict the direction of change and strength of correlation with each axis.

relatively low across islands except for between Seguam and Samalga Passes, where a decrease in salinity was seen around Yunaska and eastward [48]. Sea urchins exhibit variable morphology, growth, and/or reproduction depending on environmental conditions [38, 76]. Consequently, temperature and salinity can influence sea urchin barren formation by altering the timing of their spawning, grazing, growth, and/or recruitment rates [11, 26]. Additionally, water temperature can influence green sea urchin reproductive phenology [21, 77] and episodic patterns of recruitment, as exhibited by green sea urchins in the northern Gulf of Alaska ([44], this study).

In contrast to the differences in sea urchin recruitment among island groups, recruitment within island groups was generally consistent (Figures 3 and 4). Variability around the mean recruitment index among islands suggests that islands may fall into different categories of recruitment: consistent and low, variable and moderately low, consistent and high, and variable and moderately high (Figure 5). Regional differences in sea urchin recruitment could therefore be due to differences in local habitat quality or environmental conditions that influence the delivery, survival, and growth of larvae as seen in other temperate regions [78, 79]. The specific factors that determine which of the four recruitment patterns occurred at a given island were not well resolved in this study; however, much of the variation was explained by biogeographic breaks formed by the large ocean passes previously discussed, such as Samalga Pass [24, 48].

Interactions among sea urchins of different size classes could be shaping some of the observed variability in demographic patterns to the west of Samalga Pass. For example, large sea urchins could potentially displace smaller ones, impeding growth and altering behaviour [80]. Small urchins could be more cryptic and difficult to detect in the presence of large conspecifics that can cannibalize smaller individuals [81]. Cannibalism and/or competitive advantages when feeding on algae may also be supporting the large individuals

dominating sea urchin populations at the Near Islands, thus limiting recruitment through density-dependent responses. Alternative life history strategies based on biogeography [24, 48] could also explain the observed discrepancies in demography between areas west and east of Samalga Pass where green sea urchins may be experiencing faster or slower growth, dependent on available resources [76]. In urchin barrens, there is little food available to support high sea urchin densities, yet sea urchins can persist for an indeterminate length of time by reabsorbing their internal organ stores and eventually their calcified test [82], or by reducing their metabolic activity to a semidormant state [83] until resource conditions improve. Diseases are also a potential density-dependent response; however, unlike sea urchin barrens in other systems [13, 84, 85], disease outbreaks have not been documented in the Aleutian archipelago, although occasional diseased individuals were noted over the sampling years (authors, pers. obs.). While fisheries for sea urchins can impact their demographics [16], active green sea urchin fisheries across the study region were minimal to nonexistent during the study period.

Environmental variables were weakly correlated with patterns of sea urchin demography, with most of the variation in demography unexplained by the environmental factors considered in this study. It is possible that some of this unexplained variation may be explained by biological interactions with the surrounding community [86]. Differences in benthic community structure across biogeographic regions may play a role in limiting or enhancing recruitment and survival of juvenile sea urchins [25, 29, 87]. For instance, differences in the assemblage of fleshy red algae or crustose

coralline algae could strongly influence patterns of sea urchin settlement and survival via differing chemical cues [88] or by offering refuge habitat to juvenile sea urchins from non-sea urchin otter predators [34, 89] such as the predatory sea star, *Pycnopodia helianthoides* [90]. Differences in sea star assemblages have been documented across the Aleutian archipelago, with *P. helianthoides* occurring predominantly east of Samalga Pass [24, 91]. However, observations of *P. helianthoides* west of Samalga Pass, from Chuginadak to Adak, suggest that there may be occasional dispersal across Samalga Pass, or that perhaps larval *P. helianthoides* were transported by transiting vessel traffic or fishing boats. Other invertebrates, such as crabs, may also limit sea urchin survival and local abundances [34]. Differences in kelp forest communities across Samalga Pass [24] may influence predator-prey interactions and allow for top-down control of sea urchins, in the absence of sea otters, while also influencing refuge habitat for occasionally settling sea urchin recruits [29].

Our study indicates that sea otters, when sufficiently abundant, overwhelm (i.e., mask) any effects of environmental control on sea urchin population demographics. After the functional extinction of sea otters across most of the Aleutian Archipelago, however, sea urchin demographics have become more sensitive to bottom-up forcing—a pattern that will likely persist—and may increase, into the future. Given that environmentally controlled systems may be more heavily influenced by climate change, restoring keystone predator populations may prove increasingly important for buffering ecosystem function and stability in the Anthropocene.

Data Availability

The data used in this study are accessible and archived in Ebert et al. [53] and with the Biological & Chemical Oceanography Data Management Office as epibenthic community abundance [55].

Disclosure

B. P. Weitzman present address is U.S. Fish & Wildlife Service, Marine Mammals Management, Anchorage, AK 99508 USA. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government. These data have been previously published as a chapter in a dissertation [92].

Conflicts of Interest

The authors declare that they have no conflicts of interest.

Acknowledgments

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