

## Research Article

# Kelp Forests versus Urchin Barrens: Alternate Stable States and Their Effect on Sea Otter Prey Quality in the Aleutian Islands

Nathan L. Stewart<sup>1</sup> and Brenda Konar<sup>2</sup>

<sup>1</sup> School of Fisheries and Ocean Sciences, University of Alaska Fairbanks, 905 N. Koyukuk Drive, 245 O'Neill Building, Fairbanks, AK 99775, USA

<sup>2</sup> Global Undersea Research Unit, University of Alaska Fairbanks, 905 N. Koyukuk Drive, 217 O'Neill Building, Fairbanks, AK 99775, USA

Correspondence should be addressed to Nathan L. Stewart, nathan.stewart@tufts.edu

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Macroalgal and urchin barren communities are alternately stable and persist in the Aleutians due to sea otter presence and absence. In the early 1990s a rapid otter population decline released urchins from predation and caused a shift to the urchin-dominated state. Despite increases in urchin abundance, otter numbers continued to decline. Although debated, prey quality changes have been implicated in current otter population status. This study examined otter prey abundance, size, biomass, and potential energy density in remnant kelp forest and urchin-dominated communities to determine if alternate stable states affect prey quality. Findings suggest that although urchin barrens provide more abundant urchin prey, individual urchins are smaller and provide lower biomass and potential energy density compared to kelp forests. Shifts to urchin barrens do affect prey quality but changes are likely compensated by increased prey densities and are insufficient in explaining current otter population status in the Aleutians.

## 1. Introduction

Natural communities can exist at multiple stable points in time or space [1]. Stable points are characterized by a specific structural and functional species assemblage recognizably different from other assemblages that can occur under the same set of environmental conditions. Such states are non-transitory, persist over ecologically relevant timescales, and are therefore considered domains of stable equilibrium [2, 3]. Although multiple stable states can exist simultaneously, communities typically alternate from one stable state to another, a shift often conveyed by a large perturbation applied directly to the state variables (e.g., population densities; [4]). Significant changes in the abundance of key species are widely cited as evidence of phase shifts ([5, 6] but see [7]) and have been documented both experimentally [8] and empirically [9, 10] in coastal marine ecosystems. In general, predator removal causes prey community shifts enabling one or few algal or invertebrate competitive dominants to proliferate.

In ecological studies in the Aleutian Islands, the presence and absence of dense sea otter populations can instigate state shifts between two alternately stable nearshore communities, one dominated by kelp and the other by sea urchins [11–13]. With sea otters present, sea urchins are reduced to sparse populations enabling kelps to flourish. With sea otters absent, dense sea urchin populations overgraze and exclude foliose macroalgae. In the early 1990s, a rapid sea otter population decline (ca. 25% per year) caused a shift in alternate stable states in the region, resulting in much of the nearshore rocky ecosystem to be dominated by urchin barrens and largely devoid of macroalgae [14]. Although urchin biomass increased during the decline [15], the sea otter population continued to decline (from ca. 77,435 in 1990 to 17,036 in 1997) and has remained at low densities (ca. 4.3 otters per km<sup>2</sup> in 1965 to 0.5 otters per km<sup>2</sup> in 2000) in the two decades since the decline [14, 16, 17]. The cause of the initial decline remains debated (starting with [15, 18, 19]), and has manifested in a debate involving two fundamentally different processes, bottom-up and top-down forcing [20]. In general,

bottom-up forcing hypotheses posit that the sea otter decline is due to changes in the availability or quality of prey (i.e., the nutritional limitation hypothesis). In contrast, top-down hypotheses posit that the decline is predator-mediated (i.e., the killer whale predation hypothesis). Sea otter diets at the population level are diverse [21] and it is argued that nutritional stress arising from changes in prey quality rather than prey quantity has not been sufficiently tested [22]. Nutritional limitation is one explanation for the decline of Steller sea lions [23, 24] and other marine predators [25] in the North Pacific and Bering Sea based on a shift from energy-rich prey to abundant energy-poor prey (the junk food hypothesis; [23, 26]). The degree to which shifts between kelp forests and urchin barrens affect prey quality and whether or not such changes could have initiated sea otter population declines and continue to limit sea otter recovery in the central and western Aleutians remains to be evaluated.

Kelp forest systems provide critical resources to nearshore marine communities in the central and western Aleutian Islands and throughout the temperate coastal zones [27, 28]. Principal resources include physical structure (habitat) and food (both directly and indirectly). Kelp forests dampen wave propagation and can mitigate the associated processes of coastal erosion, sedimentation, benthic productivity, and recruitment [29]. In addition, kelp canopies can influence interspecific algal competition by attenuating sunlight [30] and creating habitat for low-light-adapted species [31]. The structural complexity of macroalgal systems provides substratum for numerous sessile animals and algae [32, 33] and habitat for mobile organisms specialized to live and feed directly on the kelp or kelp-associated assemblages [34, 35]. Although kelps are highly productive, nutrients are primarily made available through macroalgal detritus [36, 37], while relatively little kelp production ( $\leq 10\%$ ) is consumed directly by herbivores [38]. Thus, kelp systems affect the abundance and biomass of associated species and mitigate ecological and oceanographic processes important to nutrient transfer to higher trophic levels.

Broad scale kelp deforestation can result from disease, herbivory, or physiological stress [32, 39, 40]. At lower latitudes, periodic kelp forest deforestation results from oceanographic anomalies in temperature, salinity, or nutrients that either kill kelps directly or trigger diseases that become lethal to algae [30, 38]. Coastal warming can also lead to increases in herbivory at lower latitudes [41–43]. In contrast, at higher latitudes sea urchin herbivory has been the most common agent of kelp deforestation and, despite morphological and chemical defenses in kelps, often leads to the formation of barren grounds [40, 44–47]. Intensive sea urchin grazing has both immediate, direct effects on the algal assemblage and numerous complex indirect effects on the greater community [11, 45, 48]. Although constituent species may remain the same, kelp forest and urchin barren systems support notably different assemblages in terms of species abundance, biomass, size distribution, and individual health [15, 49]. In general, relatively few epibenthic invertebrates succeed in urchin barrens and sea urchins themselves, the competitive dominant, are likely food ([50], but see [51, 52]) and size limited [53, 54]. Sea urchins size limitation in urchin barrens has

been attributed to both the natural organization of urchin feeding aggregations (e.g., larger urchins lead feeding fronts in kelp beds and smaller urchins occupy adjacent barren zones; [54]) and poor nutritional resources in barrens [52]. The lack of structural habitat complexity associated with urchin barrens can lead to increased predation and further affect prey abundance, biomass, and size. Experimental studies with tethered crabs and observational studies of fishes in kelp beds of varying complexity have shown that predation rates are a function of both kelp presence and architectural complexity. In general, larger and more abundant crabs and fishes are associated with more complex algal structure [55, 56]. Consequently habitats lacking kelp harbor smaller prey and are relatively unproductive compared to those with kelp [13].

Shifts to urchin barren stable states often entail an ecosystem service and function loss (for review see [6]). This is seen in the nearshore where decreases in the proportion of kelp to barrens have led to coastal consumer decreases [37], reduced interaction strengths between predatory sea stars and their invertebrate prey [57], and altered fish abundances and diets [58]. In the Aleutian Islands, kelp removal by sea urchins had negative effects on bald eagle, glaucous-winged gull, benthic-feeding sea duck, harbor seal and fish abundance [11, 59, 60], declines attributed to poor nearshore energy returns, and kelp forest habitat loss. Predator declines initiated by phase shifts have been linked to diminished prey resources in many nearshore marine systems [9, 61, 62]. To date, research focusing on alternate stable states has predominantly used predator abundance, diet analyses, or behavior to describe cascading effects associated with shifts to “less-desirable” states [6]. Very few studies have focused directly on individual prey attribute changes associated with phase shifts. Notable exceptions include documented declines in gamete production [63], prey palatability [64], and altered growth rates [65]. Although several studies have used sea urchin gonad indices to test for food limitation in urchins [50, 52], no studies to date have described changes in the biomass, size, and potential energy density of prey associated with shifts between kelp forests (productive systems) and urchin barrens (less-productive systems). Sea urchins have been shown to exhibit slower growth rates in barrens compared to kelp beds [66]. The persistence of remnant kelp forests in the in the current urchin barren dominated stable state is likely maintained by physical processes such as algal whipping [50]; however the long-term stability of these communities is largely unknown. The cooccurrence of both remnant kelp forests and urchin barrens in the central and western Aleutians provides an opportunity to evaluate prey quality in each community and to evaluate the hypothesis that prey quality changes initiated the sea otter decline and continue to limit their recovery.

This study quantified sea otter prey quality in remnant kelp forest and urchin barren communities across a longitudinal gradient in the central and western Aleutians to determine if prey quality is affected by phase shifts and if these changes could feasibly limit sea otter recovery. Three hypotheses were developed: (1) remnant kelp forests will provide greater individual prey biomass than urchin barrens, (2) kelp forests will provide greater prey energy density per

unit area than urchin barrens, and (3) sea otters foraging in kelp forests require less predicted feeding effort to meet daily energy requirements than sea otters foraging in urchin barrens. To test these hypotheses, and the feasibility of nutritional limitation, sea otter prey abundance, biomass, size, and energy density were evaluated and then related to a foraging sea otter's daily energetic costs and to prey values from elsewhere in the sea otters range where populations are increasing or stable.

## 2. Methods

This study was carried out at eight central and western Aleutian Islands in Alaska (Figure 1). The study spanned a 460 nm longitudinal gradient, from Atka Island (52° 20' 6N, 174° 7' 1W) to Alaid Island (52° 45' 2N, 186° 5' 8E), and was sampled in June of 2009 and July of 2010. Sites ( $n = 8$ ) were selected based on a definitive kelp-barren interface ( $\geq 30$  m long) containing dense understory kelp ( $\geq 5$  stipes·m<sup>-2</sup>). Sites were sampled at mean sea otter foraging depths (10–15 m, [67]) and consisted of continuous bedrock or large stable boulder substratum. Cryptic habitats such as deep crevices or loosely piled boulders capable of harboring small sea otter prey species were rare or absent.

To determine if alternate stable state communities provide similar sea otter prey abundance, size, and biomass, forty randomly placed 0.25 m<sup>2</sup> quadrats were sampled within urchin barrens ( $n = 20$ ) and adjacent kelp forests ( $n = 20$ ) at each island. All kelp stipes, including *Laminaria saccharina*, *Agarum cribrosum*, *Thalassiphyllum clathrus*, *Cymathere triplicate*, and *Laminaria yezoensis*, occurring within quadrats were counted in kelp forests before sampling to ensure minimum kelp density requirements were met. Sea otter prey species, which included sea urchins (*Strongylocentrotus polyacanthus*), mussels (*Mytilus trossulus*), rock jingles (*Pododesmus machrochisma*), discordant mussels (*Musculus discors*), and hairy tritons (*Fusitriton oregonensis*), occurring within quadrats were counted. Scat analysis and focal observations suggest that these species are the dominant sea otter prey in the region [13, 45]. Fishes are a component of sea otter diets in the region but are generally less preferred prey [45, 60] and, in the case of smooth lumpfishes, are episodic in their contribution sea otter diet [68] and were therefore not included in this analysis. Prey size was determined by measuring the maximum test or shell linear diameter of all prey encountered within each quadrat. In addition to counts and size measurements within quadrats, subsamples of sea urchins ( $n = 10$  per community per island) and other prey species ( $n = 5$  per community per island due to lower abundances) were collected from each quadrat (ADFG Permit No. CF-08-016 and CF-09-028). Only the largest individuals of each species occurring within quadrats were collected to simulate size selective foraging behavior exhibited by sea otters [69, 70]. Biomass per individual prey species was determined using test or shell-free wet weight from collected prey and is expressed in terms of g wet mass (WM) per individual. Biomass per unit area (g WM·0.25 m<sup>-2</sup>) was calculated using species-specific size to biomass conversion factors [71, 72] and calibrated using size to biomass values from specimens collected in this study.

To determine if alternate stable state communities provide similar sea otter prey energy density per individual and per unit area, the caloric content of sea otter prey species was determined using bomb calorimetry. In preparation for ash weighing and caloric content analysis, a random subsample of test and shell-free wet samples from collected prey ( $n = 3$  per species per community per island) were oven dried at 110° for 24 h and finely pulverized into powder. Ashing was carried out in a muffle furnace at 500° for 4 h. Weight loss from ashing was regarded as organic content and used to express the caloric content in terms of ash-free dry weight (AFDW). Homogeneous dry samples were formed into pellets and calorimetric determinations were made with both a Parr model 6200 Isoperibol bomb calorimeter with an 1108 oxygen bomb and 6510 water handling system. Energy from dry matter (cal·g<sup>-1</sup> DM) was then multiplied by the proportion of dry matter in the wet mass to express potential energy density in terms of wet mass (kcal g<sup>-1</sup> WM) per individual prey. Potential prey energy density per unit area (kcal·g<sup>-1</sup> WM·0.25 m<sup>-2</sup>) was calculated using species-specific biomass to energy density conversion factors [71, 72] and calibrated using values from specimens collected in this study. Although wet mass is influenced by ash and water dilution, it is a better representation of the actual prey biomass consumed by sea otters [72].

To determine if sea otters foraging in kelp forests require less predicted feeding effort to meet the daily energy requirements than sea otters foraging in urchin barrens, sea otter prey variables were compared to the activity budget and metabolic rate of a typical 34 kg male sea otter from the central and western Aleutians [73]. Prey abundance, size, and energy density were related to sea otter daily energy requirements to calculate predicted feeding effort required to meet daily caloric needs foraging in each community. Predicted feeding effort was calculated in terms of both percent time needed in a 24-hour period to meet daily caloric needs and in terms of the number of individual urchins needed to meet daily caloric needs. Sea otter prey assimilation efficiency was standardized at 82% efficiency [74] and feeding rates were standardized at 1.9 urchins·min<sup>-1</sup> for kelp forests and 3 urchins·min<sup>-1</sup> for urchin barrens, respectively (USGS, unpublished data).

To determine if prey quality values in the central and western Aleutians are limiting current sea otter recovery, potential prey energy density values measured in this study were compared to species-specific energy density determinations from locations where sea otter populations are currently increasing (Kachemak Bay Alaska; Stewart and Konar, unpubl. data, [75], Glacier Bay Alaska; [72, 76], and San Nicholas Island California; [72, 77]) or stable (Monterey Bay California; [21, 72]). Direct comparisons between sea otter prey species were made at the species level with the exception of *Strongylocentrotus polyacanthus* (Aleutians) and *S. droebachiensis* (elsewhere in Alaska and California) due to the similarities in the size and potential energy density of these two species [78].

**2.1. Data Analysis.** Differences in prey abundance, biomass, size, and energy density between communities were examined using ANOVA ( $\alpha = 0.05$ ) with communities as

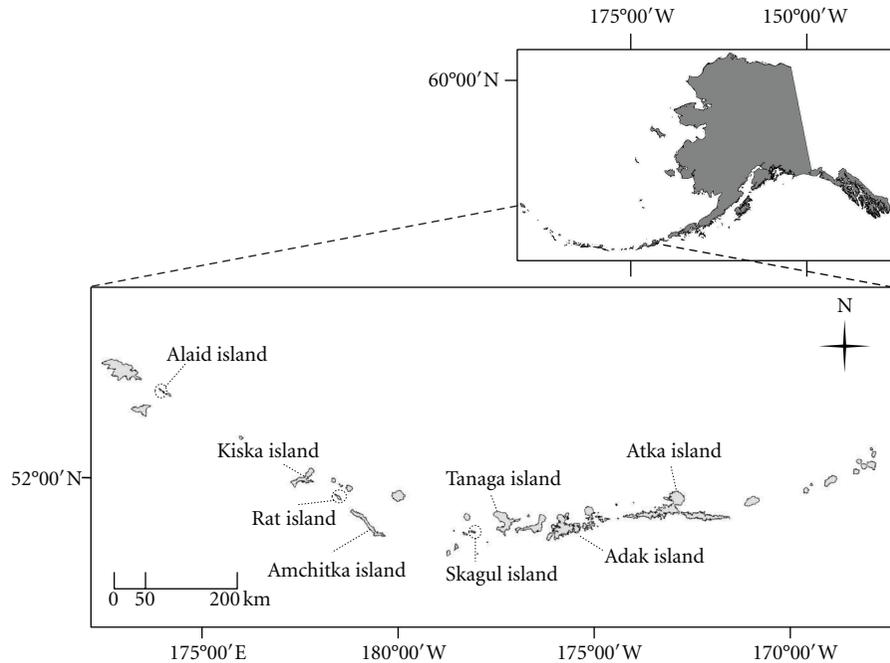


FIGURE 1: Map of the central and western Aleutian Islands, Alaska (inset), indicating the eight islands sampled in this study.

TABLE 1: Kelp density and sea otter prey abundance (individuals per 0.25 m<sup>2</sup>) in kelp forest and urchin barren communities in the central and western Aleutian Islands, Alaska.  $\bar{N}$  is the mean of prey species counted within 0.25 m<sup>2</sup> quadrats in each community ( $n = 8$  islands with 20 quadrats per community per island). Prey species include *Strongylocentrotus polyacanthus* (*Strongylo.*), *Pododesmus machrochisma* (*Pododes.*), *Mytilus trossulus* (*Mytilus*), *Musculus discors* (*Muscul.*), and *Fusitriton oregonensis* (*Fusitrit.*). Significant differences from Tukey post hoc comparisons  $P \leq 0.05$  level are indicated by (\*). NP: Not present.

	Kelp density (inds.·0.25 m <sup>-2</sup> )	$\bar{N}$	Abundance (inds.·0.25 m <sup>-2</sup> )				
			<i>Strongylo.</i>	<i>Pododes.</i>	<i>Mytilus</i>	<i>Muscul.</i>	<i>Fusitrit.</i>
Kelp	5.89 ± 1.14	1.6 ± 1.1	3.8 ± 1.9*	2.3 ± 1.2	0.9 ± 0.7	0.8 ± 1.1	0.2 ± 0.1
Barren	NP	6.5 ± 2.3	28.6 ± 5.8	2.5 ± 1.5	1.1 ± 0.6	NP	0.3 ± 0.1

treatments (e.g., remnant kelp forests and urchin barrens) and means from quadrats within communities as replicates. When significant effects were found in ANOVA, post hoc comparisons were made using Tukey's Honestly Significant Difference (HSD) test. Multivariate analysis was used to illustrate differences in urchin barren and kelp prey communities attributable to prey availability, quality, and size (PRIMER-E v.6, [79, 80]). Prior to analyses, data were square root transformed to reduce the dominant contributions of abundant species and a similarity matrix of all samples was produced using a Bray-Curtis index. The similarity between urchin barren and kelp communities was assessed in terms of prey variables using multidimensional scaling ordination. Similarity percentages analysis (SIMPER) was used to determine which taxa contributed most to the observed dissimilarity among urchin barren and kelp communities represented by the euclidean distances between sites.

### 3. Results

Kelp forest and urchin barren prey communities were clearly delineated by differences in kelp and macroinvertebrate

abundance (Table 1). Urchin barrens provided significantly more abundant prey than remnant kelp forests (ANOVA,  $n = 8$ ,  $F = 132.1$ ,  $P < 0.001$ ). Tukey post hoc comparisons indicated that *Strongylocentrotus polyacanthus* abundance was significantly different between kelp forests and urchin barrens. Dense *S. polyacanthus* populations comprised the bulk of available prey (45.5 to 87.9%) in both communities but were seven times more abundant in barrens ( $28.6 \pm 5.8$  inds·0.25 m<sup>-2</sup>) than in remnant kelp forests ( $3.8 \pm 1.9$  inds·0.25 m<sup>-2</sup>). When present, *Musculus discors* was more abundant in kelp forests ( $0.8 \pm 1.1$  inds·0.25 m<sup>-2</sup>) than urchin barrens (none present); however this species only occurred at three of the eight islands. The rock jingle, *Pododesmus machrochisma*, was consistently abundant at low densities in both communities. The remaining prey species, *Mytilus trossulus* and *Fusitriton oregonensis*, showed patchy distributions or were equally present in both kelp forests and urchin barrens. No significant differences were detected in nonurchin prey size kelp forest and urchin barren communities (ANOVA,  $n = 8$ ,  $F = 2.02$ ,  $P = 0.33$ ).

Kelp forests supported significantly larger urchins ( $54.1 \pm 21.4$  mm) than barren habitats ( $47.1 \pm 17.3$  mm; ANOVA,

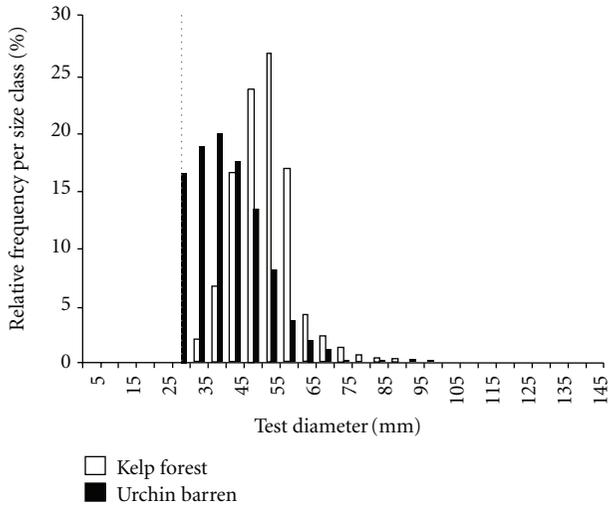


FIGURE 2: Relative frequency distributions of sea urchins (*Strongylocentrotus polyacanthus*) collected in remnant kelp forest and urchin barren communities in the central and western Aleutian Islands. Relative frequency percentages are determined using counts from sea urchins in kelp forests ( $n = 308$ ) and urchin barrens ( $n = 4569$ ). The dotted line indicates the minimum size threshold for sea otter predation on urchins (30 mm).

$n = 8$ ,  $F = 5.34$ ,  $P = 0.02$ ; Figure 2). Kelp forests provided significantly higher biomass per individual urchin than barrens (ANOVA,  $n = 8$ ,  $F = 39.1$ ,  $P = 0.016$ ; Figure 3). Urchin barrens, however, provided significantly higher biomass per unit area compared to remnant kelp forests (ANOVA,  $n = 8$ ,  $F = 97.9$ ,  $P < 0.001$ ). Although constituent reproductive tissue biomass was significantly greater in individual urchins in kelp forests ( $0.05 \pm 0.02 \text{ kcal} \cdot \text{g}^{-1}$  per urchin) than urchin barrens ( $0.02 \pm 0.01 \text{ kcal} \cdot \text{g}^{-1}$  per urchin, ANOVA,  $n = 8$ ,  $F = 22.2$ ,  $P = 0.04$ ), differences in available reproductive tissue per unit area were not significant (ANOVA,  $n = 8$ ,  $F = 0.84$ ,  $P = 0.31$ ). Individual urchins in kelp forests provided significantly higher potential energy density ( $0.21 \pm 0.02 \text{ kcal} \cdot \text{g}^{-1}$  per urchin) compared to urchin barrens ( $0.14 \pm 0.08 \text{ kcal} \cdot \text{g}^{-1}$  per urchin, ANOVA,  $n = 8$ ,  $F = 26.6$ ,  $P = 0.03$ ; Figure 4). In contrast, urchin barrens provided significantly greater potential energy per unit area than kelp forests (ANOVA,  $n = 8$ ,  $F = 107.2$ ,  $P < 0.001$ ). Potential energy density values of individual prey species ( $\text{kcal} \cdot \text{g}^{-1} \text{ WM} \cdot \text{ind.}^{-1}$ ) from both communities in this study were comparable to values from other studies conducted elsewhere in the sea otters range (Table 2).

A typical sea otter in the central and western Aleutians could easily meet daily energy requirements foraging in either kelp forest or urchin barren communities. A 34 kg male sea otter has a daily energy requirement of approximately  $4600 \text{ kcal} \cdot \text{day}^{-1}$  [73]. Due to differences in the abundance, size, and energy density of urchins from remnant kelp forests and urchin barrens, a typical Aleutians sea otter would need to consume 484 urchins in a kelp forest (18% time, feeding rate of  $1.9 \text{ urchins} \cdot \text{min}^{-1}$ ) versus 1085 urchins (25% time, feeding rate of  $3 \text{ urchins} \cdot \text{min}^{-1}$ ) in an urchin barren to

meet daily caloric needs [72, 73]. The differences in percent time required to meet daily caloric needs foraging in either community are well below those seen in populations where food resources are limiting, such as central California where male sea otters spent 25–40% time feeding [73, 77]. In addition, given comparable feeding rates foraging in either community, the number of urchins required to meet daily caloric needs is well within the actual number observed in empirical studies of foraging sea otters (e.g., [68]).

Sea otter prey abundance, size, biomass, and energy density contribute to the separation in urchin barren and kelp forest prey communities in multidimensional scaling analyses (MDS; Figure 5). The separation between prey communities was driven by significantly higher total prey biomass and potential energy per unit area associated with dense sea urchin populations in urchin barrens (Figure 6, SIMPER, 87%). Individual urchin energy density did not contribute significantly to the separation in sites (SIMPER, 9%).

#### 4. Discussion

In its current stable state, the nearshore community in the central and western Aleutian Islands is dominated by abundant but low-quality prey. Expansive urchin barrens support dense sea urchin populations that are generally contain smaller individuals and provide less biomass and energy density per individual than kelp forest urchins. Interspersed in the system is a patchwork mosaic of remnant kelp forests that support relatively few but large, calorically rich sea urchins. Though statistically significant, the difference in individual sea urchin potential energy density in kelp forests and urchin barrens is likely to be biologically inconsequential to foraging sea otters. Potential urchin energy density values measured in this study indicate that an average kelp forest urchin is equal to approximately one and a half barren urchins in terms of edible wet biomass and energy content. Given sea urchin feeding rates and assimilation efficiency [73], sea otter daily energy requirements are easily met foraging in either community. Although individual prey quality changes likely occurred during the shift from kelp forests to urchin barrens during the 1990s sea otter decline, these changes are unlikely to have caused the sea otter decline nor are they limiting current sea otter recovery. Both kelp forest and urchin barren urchins sampled in this study are comparable to potential energy density values of individual urchins elsewhere in the sea otter's range [72]. In addition, all other sea otter prey evaluated in this study, with the exception of *Musculus discors*, did not vary in abundance, size, biomass, or energy density between kelp and barren communities. Consequently, though changes in prey quality associated with phase shifts represent an ecosystem service loss to predators, this loss is likely compensated by increases in prey abundance and total available biomass.

Sea urchins competitively dominate nearshore communities in the central and western Aleutian Islands. Their dominance in the absence of top-down control is typical of urchin barren phase states elsewhere [9, 43, 81] and is comparable to other competitive dominants in marine systems where

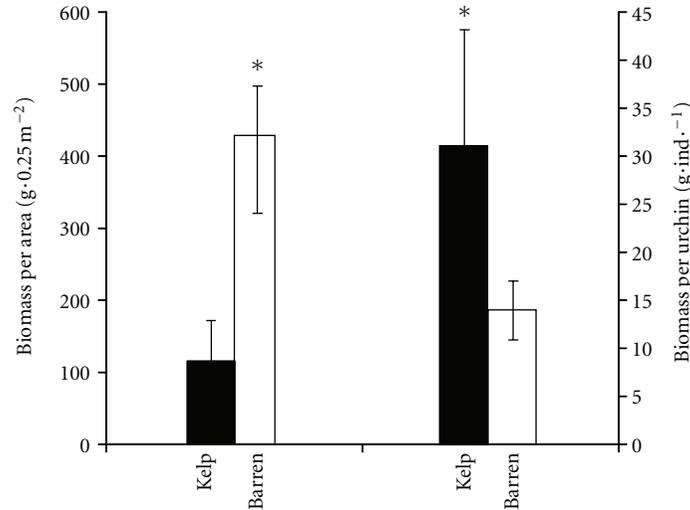


FIGURE 3: Sea urchin biomass per unit area and biomass per individual urchin from remnant kelp forest and urchin barren communities throughout the central and western Aleutian Islands. Significant differences at  $P \leq 0.05$  level are indicated by (\*).

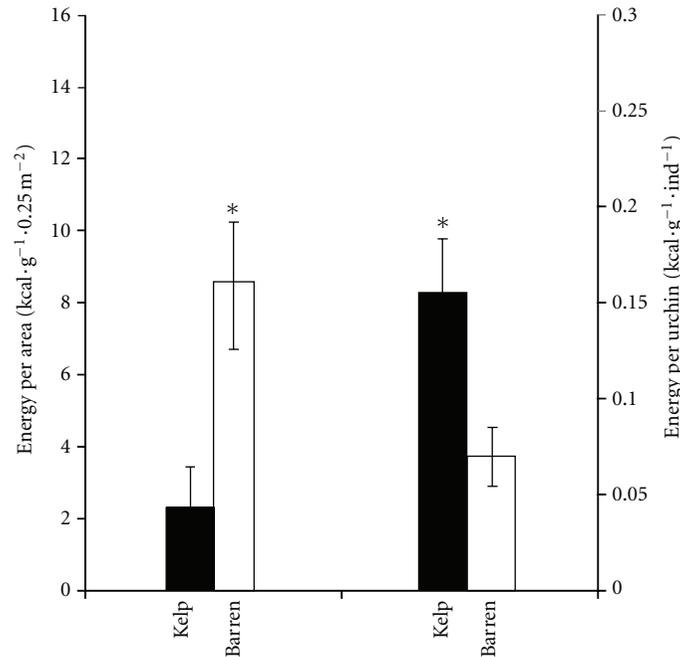


FIGURE 4: Sea urchin potential energy density per unit area and potential energy density per individual urchin from remnant kelp forest and urchin barren communities throughout the central and western Aleutian Islands. Significant differences at  $P \leq 0.05$  level are indicated by (\*).

predators have been experimentally removed, including barnacles [82] and mussels [83]. Urchin densities on barrens as sampled in this study were approximately seven times greater than those in remnant kelp forests, a pattern common throughout the Aleutian Islands during phase shifts to urchin barrens [13, 15]. Kelp forest-associated urchins were often found in the kelp blades and less commonly observed on the substrate, were larger, and provided significantly more biomass per urchin than urchins in barrens. Urchins associated with barrens, in addition to being smaller, were notably diminished in wet tissue mass and generally contained very

little to no reproductive tissue compared to kelp forest urchins. Mass differences between individual urchins were attributed both to size differences and to differences in the ratio of reproductive to nonreproductive tissue, a variable known to decrease with increasing urchin density [63] and increase with increasing macroalgal food sources [50]. Urchin reproductive tissue is significantly more energy dense than other tissues [84] and in this study translated into significantly higher energy density per individual urchin. Consequently, although urchins in kelp forests are significantly less abundant than those in urchin barrens, they provided more

TABLE 2: Individual prey quality values from remnant kelp forest and urchin barrens sampled in this study and from locations elsewhere in the sea otters range. Values indicate the potential energy density per individual species ( $\text{kcal}\cdot\text{g}^{-1}$  wet mass)  $\pm$  1 S.D. Prey species include *Strongylocentrotus polyacanthus*, *Mytilus trossulus*, and *Fusitriton oregonensis*. *S. polyacanthus* is most common in the Aleutians but is compared to *S. droebachiensis* from other regions in this table given their similarity in mitochondrial DNA analysis [78]. Current population trends were referenced in Estes et al. 2005 [17] (C. and W. Aleut., AK: central and western Aleutians, AK), Gill et al. 2009 [75] (KBay, AK: Kachemak Bay, AK), Bodkin et al. 2003 [76] (GBNP, AK; Glacier Bay, AK), Estes et al. 2003 [21] (MBNMS, CA: Monterey Bay, CA), and Tinker et al. 2008 [77] (SNI, CA: San Nicholas Is., CA). Sources of regional prey values are (A) this study; (B) Stewart and Konar, unpublished data; and (C) Oftedal et al. 2007. Sea otter population status from each location is either (D) declining, (I) increasing, or (S) stable. NP: Not present.

Location	Source	Sea otter pop. status	Prey Species		
			<i>Strongyloc.</i>	<i>Mytilus</i>	<i>Fusitrit.</i>
C., W. Aleut., AK					
kelp forest	A	D	$0.21 \pm 0.02$	$0.41 \pm 0.06$	$1.36 \pm 0.06$
urchin barren	A	D	$0.14 \pm 0.08$	$0.47 \pm 0.04$	$1.41 \pm 0.03$
KBay, AK	B	I	$0.26 \pm 0.06$	$0.36 \pm 0.02$	$1.09 \pm 0.08$
GBNP, AK	C	I	$0.24 \pm 0.04$	$0.33 \pm 0.06$	$1.11 \pm 0.23$
MBNMS, CA	C	S	$0.39 \pm 0.04$	$0.55 \pm 0.04$	NP

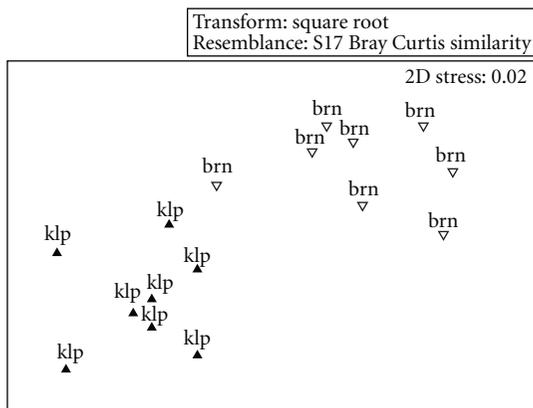


FIGURE 5: MDS ordination of the contribution of sea otter prey size, abundance, biomass, and energy density to the gradient in separation of remnant kelp forest and urchin barren communities in the central and western Aleutian Islands, Alaska. Kelp forests (klp) and urchin barrens (brn) are indicated.

biomass and potential energy density per individual. Greater sea urchin densities in urchin barrens provide greater total available prey biomass and total potential energy density due to the total mass of tissue available not the mass or quality of tissue per individual. Thus, the relationship between prey availability and quality in these two phase states is more complex than suggested by species abundances alone.

The absence of kelp did not have an effect on the distribution or density of four of the six sea otter prey species sampled during this study. Two prey species, including urchins themselves, varied in abundance with kelp presence and absence. In contrast to the inverse relationship urchins exhibited with kelp, *Musculus discors* was more abundant in kelp due to its preferred association with kelp [85]. *Musculus discors* had a nonuniform distribution and occurred in a dense but patchy distribution as seen in recruitment studies elsewhere in the North Pacific [86]. The remaining sea otter prey species sampled in this study did not show any variation in

abundance, biomass, energy density, or size as a function of community type. *Pododesmus machrochisma* provided relatively high biomass and energy density per unit area but did not vary significantly in abundance between communities. This species is conspicuous, often occurring in dense aggregations on the edges of boulders and on ledges, and is easily removed from the substrate. Both *M. discors* and *P. machrochisma* are utilized by sea otters in the central and western Aleutians (Estes and Tinker unpubl. data) and likely supplement sea urchin energy density when preferred food items such as large sea urchins are scarce [87]. *Mytilus trossulus* and *Fusitriton oregonensis* exhibited patchy distributions and did not vary significantly between communities. With the exception of the patchy distribution of the kelp-associated *M. discors*, the availability and quality of non-urchin sea otter prey sampled in this study did not vary significantly with kelp presence or absence. The covariation between *M. discors* abundance and kelp abundance, and *S. Polyacanthus* and kelp abundance, suggests that the degree to which phase shifts effect prey quality depends on the interaction strength between a particular prey species, kelp, kelp subsidies, and the distance to kelp forest-urchin barren interfaces. As a result, sea urchins, a preferred prey of sea otters and directly linked with kelp forest-urchin barren dynamics, are a strong indicator of phase shifts in the Aleutians [88]. Findings from this study further support the claim that increases in sea urchin biomass during the sea otter decline are evidence against the nutritional limitation hypothesis [15]. It also addresses the concerns by Kuker and Barrett-Lennard [22] that additional abundance data for non-urchin sea otter prey species may refute Estes et al. [15].

Given sea urchin importance to sea otter diets in the central and western Aleutians [11, 13, 89], the potential impacts of changes in sea urchin abundance, biomass, size, and energy density between phase states detected in this study deserve closer evaluation. Potential calorie availability in the central and western Aleutians varies by the prey unit exploited (e.g., individual urchin versus aggregations of urchins) and by the type of community being targeted. Currently

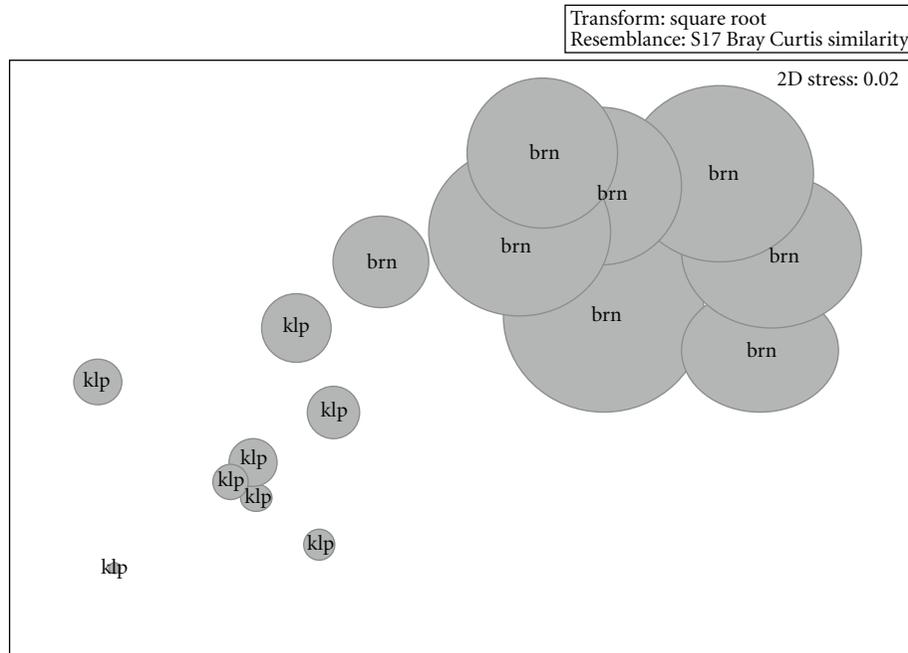


FIGURE 6: MDS bubble plot of the contribution of sea otter prey biomass to the separation in kelp forest and urchin barren communities in the central and western Aleutian Islands, Alaska. Bubble size scales with  $g \cdot 0.25 \text{ m}^{-2}$  from remnant kelp forest (klp) and urchin barren (brn) sites.

the spatially dominant community in the region, urchin barrens, supplies more nutrition per unit area but less nutrition per individual than kelp forests. Depending on a predator's foraging strategy, foraging for sea urchins in remnant kelp forest patches versus expansive urchin barrens could provide significantly different potential energy returns [90]. A predator that preferentially consumes larger and more calorically rich individual prey at the cost of increased search time in kelp understory would benefit from the selective use of kelp forest patches. Cormorants exhibit this foraging strategy in their selection of dense kelp-forested areas as opposed to recently kelp-harvested areas in Norway, despite significant increases in foraging times associated with locating fish in kelp [91]. This strategy is only feasible until the point at which the nutritional advantages of targeting prey in complex environments are outweighed by the cost of increased search time [90]. In contrast, a predator that exhibits general foraging behavior would likely exploit urchin barrens habitually and opportunistically forage in kelp forests. This strategy is exhibited by fish-eating killer whales that generally hunt in open water but occasionally specialize their foraging behavior and work cooperatively to take salmonid prey seeking refuge in dense kelp beds [92]. Sea otters are size selective foragers that generally select the largest and most calorically rich prey first before switching to smaller or less preferred prey species [69, 93]. Theoretically, a community dominated by small, low-quality prey could alter predator movement [94], lead to abandonment for areas with greater potential energy density [95, 96], or result in starvation and population decline; however, given the subtle differences in individual and areal potential energy density, these scenarios

are unlikely with sea otters. Sea otters have large energy requirements due to an elevated metabolic rate [89, 97] and as a result ingest 20 to 25% of their body mass in prey per day [74, 89] and spend 23 to 50% of the day foraging [98–100]. Although sea otter feeding rates on sea urchins differ in kelp forests (ca.  $1.9 \text{ urchins} \cdot \text{min}^{-1}$ ) and urchin barrens (ca.  $3 \text{ urchins} \cdot \text{min}^{-1}$ ) due to increased search times associated with foraging in kelp (Estes and Tinker, unpublished data), daily energy requirements are easily met foraging in either remnant kelp forest or urchin barren communities. Given sea otter activity budgets, metabolic rates, and distances travelled during foraging [73, 101, 102], the differences in individual sea urchin size and available biomass among kelp forest and urchin barrens are likely negligible to foraging sea otters. Numerous examples of expanding sea otter populations have reported otters continuing to forage in areas of depleted prey rather than moving to adjacent sites with larger individual prey and higher overall prey abundances [103, 104]. Furthermore, though depleted individual sea urchin quality values detected in urchin barrens in this study were lower than urchin values from locations where sea otter populations are currently increasing or stable, a difference of such small magnitude (ca.  $0.07 \text{ kcal} \cdot \text{g}^{-1}$ ) is not likely to affect sea otter resource selection. Consequently, despite the differences in individual prey abundance, biomass, size, and energy density between kelp forests and urchin barrens in the central and western Aleutians today, nutritional limitation is not likely to affect potential sea otter recovery to the region.

In conclusion, the phase shift between kelp forest and urchin barrens not only has an effect on kelp and urchin abundance and biomass but has also further effects on both

individual and total potential energy density provided by urchins. In support of the first hypothesis, remnant kelp forests provide greater individual prey biomass than urchin barrens. Kelp forests do not, however, provide greater energy density per unit area than urchin barrens as was predicted in the second hypothesis. Prey quality differences were, however, not significant enough to explain the rate of sea otter population declines reported during the 1990s (ca 25% per year; [15]) nor are they sufficient to explain the persistent limitation of sea otter recovery in the two decades the decline. Given what is known about sea otter foraging behavior, gross daily metabolic needs, and prey availability, it is not feasible that sea otters were or are currently nutritionally limited in the central and western Aleutians. Although the capacity of sea otters to exploit sea urchin hyperabundance and recolonize their historical range is indisputable from both practical [104, 105] and conceptual standpoints [106], the ecosystem wide effects of alternating between energy-poor and energy-rich equilibrium points likely have effects on resource selection and ultimately the carrying capacity of other consumers in the central and western Aleutians. This study indicates that the overall potential energy density provided by kelp forests is diminished when urchin barrens are temporally and spatially dominant, as has been speculated for urchin barrens elsewhere [52]. Phase shifts in kelp forest-urchin barren systems have effects on the potential prey energy density available to higher trophic levels and, in addition to statistical differences in the abundance of key species, could provide a further means to differentiate between equilibrium states.

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