The sea urchin – the ultimate herbivore and biogeographic variability in its ability to deforest kelp ecosystems

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Abstract

Barren rocky seafloor landscapes, denuded of almost all life by ravenous sea urchins, liberated from their predators, stands as one of the iconic images of trophic cascades in Ecology. While this paradigm has been cited in nearly every temperate rocky reef ecosystem across the globe, there is widespread disagreement as to its generality. Given their biology, sea urchins are clearly one of the ocean's strongest herbivores in many systems, but where will their impact be strongest? Here we perform a global meta-analysis of sea urchin-kelp relationships in the field. We find that sea urchins appear to be able to control kelp abundances in any system where they can achieve high densities. Furthermore, their ability to create large-scale long-lasting barrens appears to be limited to biogeographic regions where they can achieve high consumptive potential. Based on

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the literature, we outline a conceptual model that examines when and where sea urchins should be able to have a strong regulating impact on kelp forest ecosystems. We suggest that many elements of global change may shift the balance of forces regulating sea urchin consumptive potential in these ecosystems. Given their ability to have strong impacts on temperate rocky reefs, these drivers need to be considered in concert with their effect on sea urchins when attempting to predict future change to marine ecosystems.

Introduction

Runaway consumption of kelp by sea urchins released from predation stands as one of the icons of top-down control within the field of Ecology. Within marine temperate ecosystems, a variety of herbivores are capable of denuding undersea landscapes of nearly all primary producers (e.g., North, 1971; Harrold & Reed, 1985; Tegner & Dayton, 1991; Ling *et al.*, 2009). None, however, are so ubiquitous in their effect across the globe as sea urchins (Estes *et al.*, 1978; Duggins, 1980; Chapman, 1981; Wharton & Mann, 1981; Breen *et al.*, 1982; Hagen, 1983; Dayton, 1985; Harrold & Reed, 1985; Jon, 1987; Andrew, 1991; Hjorleifsson *et al.*, 1995; Dotsu *et al.*, 1999; Gagnon *et al.*, 2005; Vasquez *et al.*, 2006; Yoneda *et al.*, 2007). Whereas extensive deforestation occurs in other ecosystems (Milchunas & Laurenroth, 1993), this ecological phenomenon occurs in kelp ecosystems over such large temporal and spatial scales that deforested areas are often considered to be alternative stable states (Johnson & Mann, 1988). However, there is a wide degree of variability across the globe as to where these ‘urchin barrens’ can occur and whether they are able to persist beyond a few months (e.g., Andrew, 1993; Connell & Irving, 2008). While deforestation may be a regional phenomenon, understanding local variation in sea urchin and kelp distributions in different biogeographic provinces may illuminate key characteristics of local kelp-urchin ecology that can enhance susceptibility of kelp systems to deforestation.

To interpret these patterns, they must be viewed through the lens of sea urchin biology and ecology. Evolutionary forces have shaped the astonishing biology of sea urchins to make them into the ultimate undersea grazer. Essentially, sea urchins are spiny hollow balls with a mouth. Aside from a water vascular system used to control their tube feet, their body contains little more than a digestive tract and gonads. Most are facultative drift feeders, capable of building up a tremendous biomass by catching passing drift algae on their spines from the highly productive surrounding environment (Mann & Breen, 1972; Vadas, 1977; Ebeling *et al.*, 1985; Agatsuma & Kawai, 1997; Rodríguez *et al.*, 2001; Day & Branch, 2002; Mathew & Gary, 2005). Young sea urchins often settle in the spine canopy of adults (Duggins, 1981), further increasing local population densities. Sea urchins can also be tremendously long-lived (the red urchin Strongylocentrotus franciscanus can live for over 100 years Ebert & Southron, 2003). Unless urchin density and biomass is reduced by external influences (Table 1), these factors can lead to persistently large sea urchin populations and biomass.

When detrital inputs become limiting, a buildup of sea urchin biomass can become problematic. Without a detrital food supply, sea urchins behaviorally switch to active roaming and scraping of the substratum (Harrold & Reed, 1985). Given their history of buildup at a site, the grazing intensity of actively roaming and scraping sea urchins may be significantly greater than one would expect given local conditions during barren formation. Sea urchins can then maintain barrens despite the limited energy available via two means. They can shrink their tests, and reabsorb body tissues (Ebert, 1968; Levitan, 1988). For nutrition, they can make use of both new algal growth and absorb dissolved organic carbon directly from the water column (Pearse & Pearse, 1973). These aspects of their biology allow sea urchins to tolerate limited food supply in newly denuded areas, and continue inhibiting kelp from recolonizing an area.

The formation of large, long-lasting sea urchin barrens, however, is not a ubiquitous phenomenon (Schiel & Foster, 1986). This may be due to sea urchins having to both behaviorally shift to active roaming and scraping of kelps and other algae from the benthos – something under control of both current ecological circumstance and evolutionary history – and for several other factors to align so that actively grazing sea urchins are not under risk of predation (Figure 1).

Where and when these factors combine to make sea urchins important in controlling the abundance of kelps around the globe is not generally known. Rather, discussions have centered on examples of individual reefs or sites of over-grazing, many of which have been considered the norm for understanding the ecology of kelp forests. Here we seek to bring together the available evidence of relationships between sea urchin abundance, kelp abundance, and sea urchin consumptive potential in the literature. We synthesize these results in a global meta-analysis, show widespread variation in the propensity of sea urchins to form barrens, and suggest that a mix of evolutionary history, community ecology, and organismal ecology is necessary to accurately predict the probability of sea urchin barren formation.

Methods

Signals of Top-Down Herbivore Driven Control

As there has been a great deal of debate regarding generality of the paradigm that sea urchins control kelp abundances, we performed a meta-analysis to examine the relationship between the abundance of kelp and sea urchins. We searched the literature for 18 global biogeographic regions (see Table 1) where kelp and sea urchins co-occur. We reviewed the literature for each biogeographic regions searching ISI Web of Science using the search terms “kelp*” and “urchin*” and the name of either the region, or various localities within the region (e.g., “Ireland” and “England” for the Western Atlantic). We also searched Google Scholar with the terms “kelp”, “urchin”, and the name of the region, as well as querying local experts for additional data. In addition, we included the data from the PISCO surveys for the Eastern Pacific as well as the National Park Service Kelp Forest monitoring data for Southern California. To be included in the meta-analysis, studies had to report both a density of sea urchins that could be transformed to number of sea urchins per square meter and either the density of kelp in number of stipes per square meter or the percent cover of kelp. We used both metrics as, depending on the biology of the local kelp species, one metric may be a better indicator of kelp standing stock (e.g., *Macrocystis pyrifera* versus *Laminaria saccharina)*. Unlike other kelps, species in the genus *Macrocystis* can have multiple blade-bearing stipes per individual plant. Therefore, for any *Macrocystis* species, the paper needed to include stipe densities or both an average number of plants per square meter and estimates of the mean number of stipes per plant.

For both kelp density and cover, we examined the relationship between kelp and sea urchins using two methods. First, we performed a linear multilevel model with the slope and intercept of the log(kelp) and sea urchin relationship varying by biogeographic area and the identity of the study (many studies covered multiple areas). While this yielded results qualitatively similar to our second analysis (the slope of the relationship varied greatly by Biogeographic Area), we found that the parameter estimates of the slopes were likely influenced by different biogeographic areas having radically different ranges of sea urchin densities. As such, we deemed it more conservative to perform a separate regression for each biogeographic area. We therefore fit data for each area using generalized linear model with a log link and a Gamma error distribution, as continuous measurements of kelp density were never less that 0 and variance tended to increase with the mean. While the estimates of slopes varied greatly, the important quality we were interested in is whether the slope was positive or negative for each area.

Sea urchin Consumptive Potential and Kelp Abundance

Sea urchin density may be insufficient to explain patterns of kelp abundance, as sea urchins from different geographic locales may have very different foraging rates on kelp due to evolutionary history. Low densities of sea urchins that can consume vast quantities of kelp may have a far larger impact on kelp than high densities of sea urchins with a minimal consumptive ability.

To examine the relationship between sea urchin consumptive potential and kelp abundance, we examined the reference list from our literature search for any studies that performed laboratory feeding assays of sea urchins and kelp. From each study, we extracted maximum consumptive ability, measured as the annualized rates of grams of kelp carbon consumed per individual urchin. When necessary, biomass of kelp consumed was converted from wet mass to dry mass assuming a dry mass:wet mass ratio of 0.15 and a dry mass:carbon mass ratio of 0.3 (approximate values based on Mann, 1972). We then created an index of sea urchin consumptive potential (i.e., measuring how strong sea urchin consumption of kelp could be) by multiplying our sea urchin density data by the laboratory-measured maximum annualized sea urchin consumption rate (grams C kelp / urchin / year) for the corresponding region. Feeding trial data were only available for 11 biogeographic regions (11 regions). For these regions, we examined the relationships between the regional mean sea urchin consumptive potential and both the regional mean and regional standard deviation of reported kelp densities in our meta-analysis. We also examined the relationship between the regional mean and regional standard deviation of our consumption index. All relationships were fit using a generalized linear model with a Gamma error and an identity (i.e., linear) link function. We transformed mean kelp densities by adding 1 in order to meet the assumptions of the error distribution.

To examine whether temperature variability may play a role in variation in either consumptive potential or kelp abundance, we also fit generalized linear models with the standard deviation in regional seawater temperature as a predictor and the standard deviation of kelp abundance. The standard deviation of seawater temperature was obtained as the standard deviation of monthly climatological means of near-surface seawater temperature in each region, as recorded in the World Ocean Database 2001 (Conkright *et al.*, 2002). The WOD01 contains in situ measurements of temperature by a variety of instruments primarily from the early 1900's through 2001, optimally interpolated to standard depth levels (Conkright *et al.*, 2002). Regional polygons were defined as in Graham et al. (this issue). To calculate a monthly climatology for each region, a Matlab R13 script (The Mathworks Inc.) was used to find and average all recorded measurements at the surface (0m) standard level in each polygon, bin those measurements by month/year, average within each month/year, and then average over all years for each month. This model was fit with a log link function. We did the same for standard deviation of temperature and standard deviation of consumptive pressure, although given the extrapolations and potential process time-scale mismatches inherent in these comparisons, we view these results as suggestive and requiring further examination as to whether the cause was fluctuating food supply, actual metabolic fluctuations, or both.

Results

In general our results showed a great deal of variation across the globe in the relationship between sea urchin abundance and kelp abundance or cover (Figures 2 and 3, Table 2 for statistics). When present, significant relationships were typically negative. At high sea urchin densities, kelp in these biogeographic areas was rare or absent. For both cover and density, only South Australia (density) and South Africa (density) had positive slopes that were likely different from zero (p=0.058 for South Australia and p=0.004 for South Australia). In many areas, however, there was no relationship between sea urchin density and either kelp abundance or cover.

After scaling sea urchin density by mass specific consumption (i.e. consumptive ability), we found that biogeographic areas with greater consumptive ability do not necessarily have lower average kelp densities (Figure 4A). Indeed, looking at means only, it would appear that biogeographic areas with higher average consumptive have, if anything, weak support for higher consumptive ability being correlated with higher kelp densities (regression coefficient = 9.649e-04 ± 7.49e-05 SE $\chi2$=3.283 p=0.070). Areas that have a greater average degree of consumptive potential also have greater variability in both the kelp abundance (Figure 4B, regression coefficient = 0.0026 ± 0.0018 SE $\chi2$=4.6255 p=0.0315) and consumptive potential (Figure 4C, regression coefficient = 0.962 ± 0.221 SE $\chi2$=88.084 p<0.001). The standard deviation in regional temperature positively influenced variation in kelp abundance (0.5192 ± 0.1480, $\chi2$=15.724 p<0.0001) Similarly, there was weak support for a positive relationship between standard deviation in temperature and standard deviation in consumptive potential (0.4471 ± 0.2743 $\chi2$=3.298 p=0.0693).

Discussion

Sea urchin grazing is an incredibly important determinant of kelp abundance in a wide variety of coastal ecosystems throughout the globe. It is not, however, a universal phenomenon. In many temperate subtidal ecosystems, sea urchins do not appear to currently regulate kelp abundances. Ecosystems where sea urchin consumption appears to drive kelp dynamics are characterized by 1) high maximum sea urchin densities, 2) high average sea urchin consumptive potential, but also 3) high variability in kelp abundance, and 4) high variability in sea urchin consumptive potential. These patterns are linked directly to our conceptual model of when and where sea urchin grazing is important. We see that sea urchins around the globe are not able to generate barren states everywhere. In areas that lack conspicuous sea urchin-driven barrens, some factor must limit their destructive potential.

For example, the effect of some sea urchins in the very same biogeographic region are determined entirely by their feeding biology. The sea urchin *Tetrapygus niger* have a much larger and stronger Aristotele´s lantern and are less efficient at catching drifting algae as their aboral podia do not present suckers unlike *Loxechinus albus* (Contreras & Castilla, 1987). This differential feeding capacity explain why *Tetrpygus* can affect kelp abundances in certain regions. In contrast, *Loxechinus* only affects the structure of kelp populations (Vásquez & Buschmann, 1997) as it seems able to only control new recruits (Buschmann *et al.*, 2004). Thus *Loxechinus* does not satisfy the condition for high average consumptive potential.

Areas that lack strong negative relationships between sea urchin abundance and kelp abundance do not contain reefs with high densities of sea urchins. This suggests that sea urchin abundances are under some form of local control. This limitation may be direct predation. It may be low recruitment. The literature is replete with explanations in each biogeographic area as to different drivers that can reduce sea urchin densities (Table 1). High sea urchin densities therefore result when these control factors break-down, such as the canonical example of otter loss in the Aleutian Islands (Estes *et al.*, 1978). However, many biogeographic areas contain relatively fewcontrols on sea urchin densities. For example, Southern and Western Australia have few reported factors which control sea urchins where overgrazing appears to be constrained to certain environmental conditions (Ling *et al.*, 2010). Why do we find no correlation between sea urchin abundance and kelp abundance?

A lack of control on sea urchins is merely one necessary but not sufficient condition for barren formation (Figure 1). Evolutionarily, sea urchins need to have kelp as a primary food source. They need to have a high enough metabolic rate that, when detrital kelp becomes limiting, they actively roam and forage for attached kelp. Last, drift kelp needs to be actually limiting. For some species of sea urchins in some biogeographic areas, these conditions are not met. For example, for Australia's *Heliocidaris erythrogramma*, there are relatively few manifestations of barrens across its range (Connell & Irving, 2008), even where their densities are relatively high (>10m2, Ling *et al.*, 2010). Barren formation thus represents the interplay of evolutionary history, community ecology, and organismal metabolic ecology.

The data also show that the variability of kelp and sea urchins within a region may be a key to understanding the propensity of sea urchins to form barrens. Many of the ecosystems where sea urchin barrens are prominent had a high degree of variability in sea urchin abundance, consumptive potential, and kelp abundance. This variability provides a measure of how variable the population dynamics of an ecosystem can be. Systems that contained barrens had among the highest and lowest kelp abundances. Even when sea urchins were absent, the variation in kelp abundance was enormous (Figures 2 and 3). This variability in kelp abundance coupled with the ability of sea urchins to build up population densities and biomass during times of plenty may be a key to understanding where barren formation is possible. Extreme variability in bottom-up resource supply that is temporally decoupled with consumer responses may be a recipe for strong top-down control and consumer created alternate stable states. Variability in temperature regime and the concomitant mismatch between the metabolic responses of producers and herbivores (O'Connor *et al.*, 2009; O'Connor *et al.*, 2011) may also play a large role in creating scenarios where barren formation is likely. Therefore, quantification of oceanographic variation in nutrient delivery and temperature fluctuations is a key to understanding what systems may be most vulnerable to overgrazing by sea urchins. We found a signal linking variation in temperature and kelp, and a possible link between variation in temperature and variation in consumptive pressure, suggesting that such processes are likely active.

Our results show that global variation in the propensity of sea urchins to be able to denude temperate rocky reefs is not a general rule. Instead, in order to understand whether a particular area is susceptible to barren formation, one must consider 1) the evolutionary history of sea urchin-kelp interactions, 2) the presence or absence of additional factors which can reduce sea urchin consumptive pressure, and 3) the inherent variability in the ecosystem that can influence these unique grazers to build up unsustainable biomass and grazing demand. Understanding these three factors is key, as all three are impacted by human influences on marine ecosystems – be it through changes in extraction of sea urchin predators, shifts in algal harvest, or climate driven shifts in sea urchin recruitment (Ling, 2008) and sea urchin metabolism. The lack of negative relationships between sea urchins and kelp on some temperate rocky reefs today does not guarantee that top-down control will not become ecologically important under a variety of different global change scenarios. Similarly, a focus on sea urchins and their consumption may only reveal a small piece of the current ecology of many rocky coasts around the globe.

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Supporting Online Material

Supporting Online Table 1: Data used for the kelp-urchin abundance meta-analysis. Full references are included in the Supplementary References. Data from the Channel Islands National Park Service Kelp Forest Monitoring Project are labeled KFM. Data from the Partnership for Interdisciplinary Study of Coastal Oceans are labeled PISCO.

Supporting Online Table 2: Data used for the urchin consumption meta-analysis. Methods for extrapolation beyond consumption rates of individuals are described in methods, with equations included in the spreadsheet.

Supporting Online Material 1: References for Table 1

Supporting Online Material 2: References for Supporting Online Table 1.

Tables

Table 1: Factors that can control sea urchin densities in different biogeographic regions. Numbered references are from the following sources and can be found in the Supporting Online Material: 1) Duggins et al. 1989; 2) Duggins 1980, 3) Dean et al. 2000; 4) Breen et al. 1982, 5) Bowlby et al. 1988, 6) Carter et al. 2007; 7) Ebert 1968, 8) Benech 1977; 9) Otsfield 1982; 10) Ebeling and Laur 1988; 11) Pearse and Hines 1987; 12) Johnson 1971; 13) Lafferty and Kushner 2000; 14) Lester et al. 2007; 15) Shears and Ross 2009; 16) Scheibling and Stephenson 1984; 17) Miller and Colodey 1983; 18) Maes and Jangoux 1984; 19) Hagan 1995; 20) Dayton 1995; 21) Tajima and Lawrence 2001; 22) Estes and Duggins 1995; 23) Watson and Estes 2011; 24) Ebert et al. 1994; 25) Watanabe and Harrold 1991; 26) Tegner and Dayton 1981; 27) Botsford 2001; 28) Cowen 1983;

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29) Andrew 1993; 30) Johnson et al. 2005; 31) Vanderklift and Kendrick 2004; 32) Choat and Schiel 1982; 33) Lamare and Barker 2001; 34) Wing et al. 2003; 35) Leinaas and Christie 1996; 36) Raymond and Scheibling 1987; 37) Vega et al. 2005; 38) Agatsuma et al. 1998; 39) Turon et al. 1995; 40) Cowen et al. 1982; 41) Ebling et al. 1985; 42) Edwards 2004; 43) Duggins 1983; 44) Pearse 1987; 45) Barrett et al. 2009; 46) Babcock et al. 1999; 47) Andrew and Choat 1982; 48) Cole and Keuskamp 1998; 49) Dix 1970; 50) Mann and Breen 1972; 51) Keats et al. 1986; 52) Gaymer and Himmelman 2008; 53) Tarr et al. 1996; 54) Blamey et al. 2010; 55) Sala and Zabala 1996; 56) Kalvass and Hendrix 1997; 57) Rogers-Bennett et al. 1998; 58) Renolds and Wilen 2000; 59) Pfister and Bradbury 1996; 60) Carter et al. 2007; 61) Andrew et al. 2002; 62) Ramirez-Felix and Manzo-Monroy 2004; 63) Fisheries Division 2005; 64) Agriculture, Food and Fisheries 2004; 65) Castilla and Fernandez 1998; 66) Boudouresque and Verlaque 2001

Table 2: Statistical results for generalized linear model fits between sea urchin abundance and kelp abundance, either (a) density or (b) cover. We report coefficients for the relationship between urchins and kelp, the model Likelihood Ratio χ^2, and the p value for the inclusion of the urchin effect.

Figures

Figure 1: The factors that can impede barren formation. Sea urchins will actively roam and scrape if 1) evolutionarily, kelp is their primary food, 2) their metabolism requires active foraging in the absence of detritus, and 3) their drift supply is limited. Their

grazing will go unchecked if 1) predators that have evolved to be effective sea urchin predators are either 2) ineffective at predation due to an easily obtained size refuge or 3) predators are removed by human extraction. It is the active roaming and scraping behavior of sea urchins coupled with a lack of proximate controlling factors that leads to sea urchin barren formation.

Figure 2: Relationship between kelp and sea urchin abundance in a variety of biogeographic areas. Plotted curves are the result relationships different from 0 at the $p<0.05$ level. Fit was assessed from a generalized linear model with a Gamma error structure and a log link using a likelihood ratio test.

Figure 3: Relationship between kelp cover and sea urchin abundance in a variety of biogeographic areas. Plotted curves are the result relationships different from 0 at the $p<0.05$ level. Fit was assessed from a generalized linear model with a Gamma error structure and a log link using a likelihood ratio test.

Figure 4: The relationship between sea urchin consumptive ability (density scaled by average mass specific consumptive rate) and kelp density in a number of biogeographic regions. (A) Average values for each quantity plotted against one another. Lines represent 95% confidence intervals from the data. Numbers each represent a different biogeographic region. (B) The relationship between sea urchin consumptive ability and the 95% CI of kelp density. (C) The relationship between sea urchin consumptive ability and the 95% CI of consumptive ability.

Table 1

	Aleutians	Southern Alaska	Pacific Northwest	Central CA	Southern CA	Baja CA
Otters	Y[1]	Y[2]/N[3]	Y[4,5]/N[6]	Y[7,8]/N[9]	N[10]	■
Disease	■	■	■	Y[11]	Y[12,13,14]	Y[14]
Recruitment Limitation	N[22]	Y[22]	Y[23,24]	Y[11,25]	N[13,26,27]	N[11,28]
Disturbance	N[22]	Y[22]	■	Y[40]	Y[41,27,42]	Y[42]
Other Predators	Y[43]	Y[43]	Y[43]	Y[44]	Y[11,26]	Y[11]
Fishing	■	■	Y[56,57,58,59]/N[60]	■	Y[26,61]	Y[61,62]

	Eastern Australia	Southern and Western Australia	Northern New Zealand	Southern New Zealand	Northwestern Atlantic	Northeastern Atlantic
Otters	■	■	■	■	■	■
Disease	■	■	Y[15]	■	Y[16,17]	Y[18]/N[19]
Recruitment Limitation	N[29]	Y[31]/N[30]	Y[32]	Y[33,34]	N[35]	N[36]
Disturbance	■	■	■	■	■	■
Other Predators	Y[29]	Y[45]	Y[46]/N[47,48]	Y[49]	Y[50,51]	■
Fishing	N[63]	N[63,64]	N[61]	N[61]	Y[61] (Maine)/N[61] (Nova Scotia)	Y[61] (France, Ireland, Iceland)/N[61] (Spain)

	Northern Chile	Southern Chile	Japan	South Africa	Mediterranean
Otters	■	■	■	■	■
Disease	N[20]	N[20]	Y[21]	■	Y[18]
Recruitment Limitation	N[37]	Y[20]	N[38]	■	N[39]
Disturbance	Y[37]	N[20]	■	■	Y[39]
Other Predators	Y[52]	N[20]	■	Y[53,54]	Y[55]
Fishing	Y[65]	Y[26,61]	Y[61]	■	Y[66]

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Table 2

	Biogeographic Area	Coefficient	Standard Error	LR χ2	P
(a)	Aleutian Islands	-0.024	0.007	8.297	0.004
	Central CA	-0.009	0.02	0.19	0.663
	Eastern Atlantic	-0.016	0.006	8.435	0.004
	Eastern Australia	-0.435	0.104	12.503	<0.001
	Eastern Canada	-0.006	0.003	10.656	0.001
	Gulf of Maine	-0.013	0.008	3.263	0.071
	Northern Chile	0.036	0.024	2.505	0.113
	Northern New Zealand	-0.067	0.05	1.601	0.206
	Pacific Northwest	-0.079	0.176	0.103	0.749
	Sea of Japan	-0.013	0.009	1.9	0.168
	South Africa	0.237	0.064	8.473	0.004
	South Australia	0.138	0.076	3.601	0.058
	Southern Alaska	-0.164	0.043	14.312	<0.001
	Southern CA	-0.022	0.002	103.684	<0.001
	Southern Chile	-0.018	0.011	2.704	0.1
	Southern New Zealand	-0.246	0.128	3.76	0.052
	Western Australia	-0.392	1.457	0.069	0.792
(b)	Aleutian Islands	-0.007	0.004	2.819	0.093
	Central CA	0.012	0.213	0.003	0.955
	Eastern Atlantic	-3.207	1.448	1.473	0.225
	Eastern Australia	-0.042	0.014	6.481	0.011
	Eastern Canada	-0.012	0.004	8.581	0.003
	Gulf of Maine	-0.05	0.016	7.218	0.007
	Northern New Zealand	-0.165	0.046	11.141	0.001
	Pacific Northwest	-0.214	0.071	3.822	0.051
	South Africa	0.032	0.066	0.217	0.641
	South Australia	-0.15	0.212	0.502	0.479
	Southern CA	-0.029	0.002	154.412	<0.001
	Southern Japan	-0.072	0.086	0.779	0.377
	Southern New Zealand	-0.261	0.1	6.784	0.009
	Western Australia	0.216	0.275	0.632	0.427

Figure 1

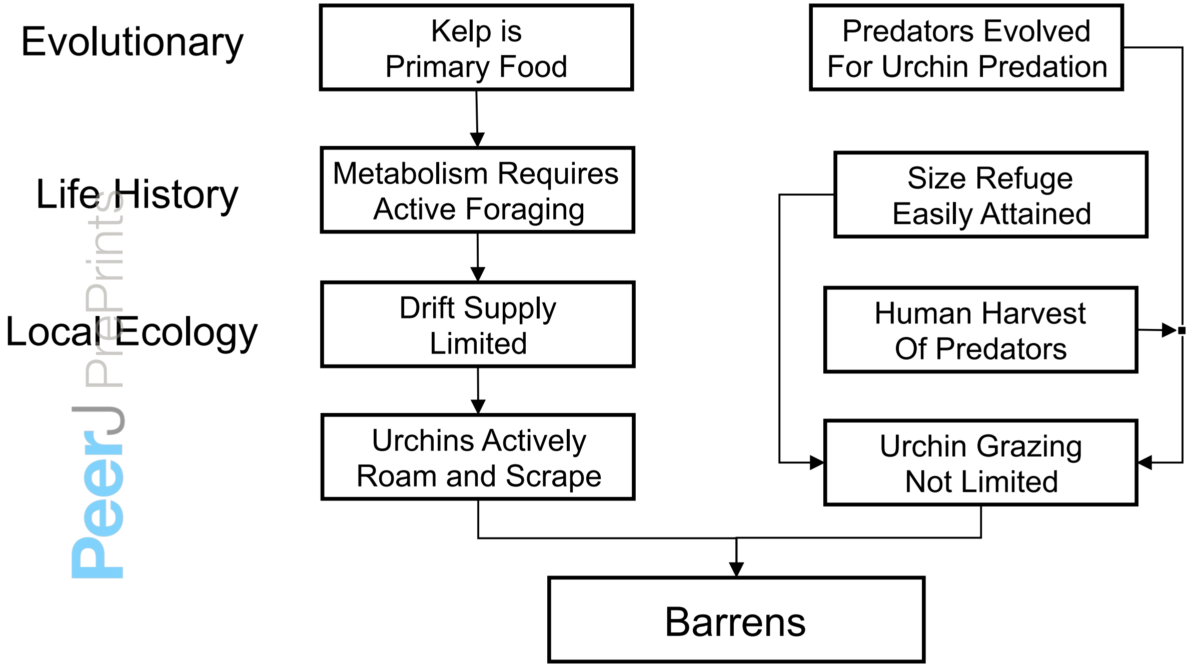

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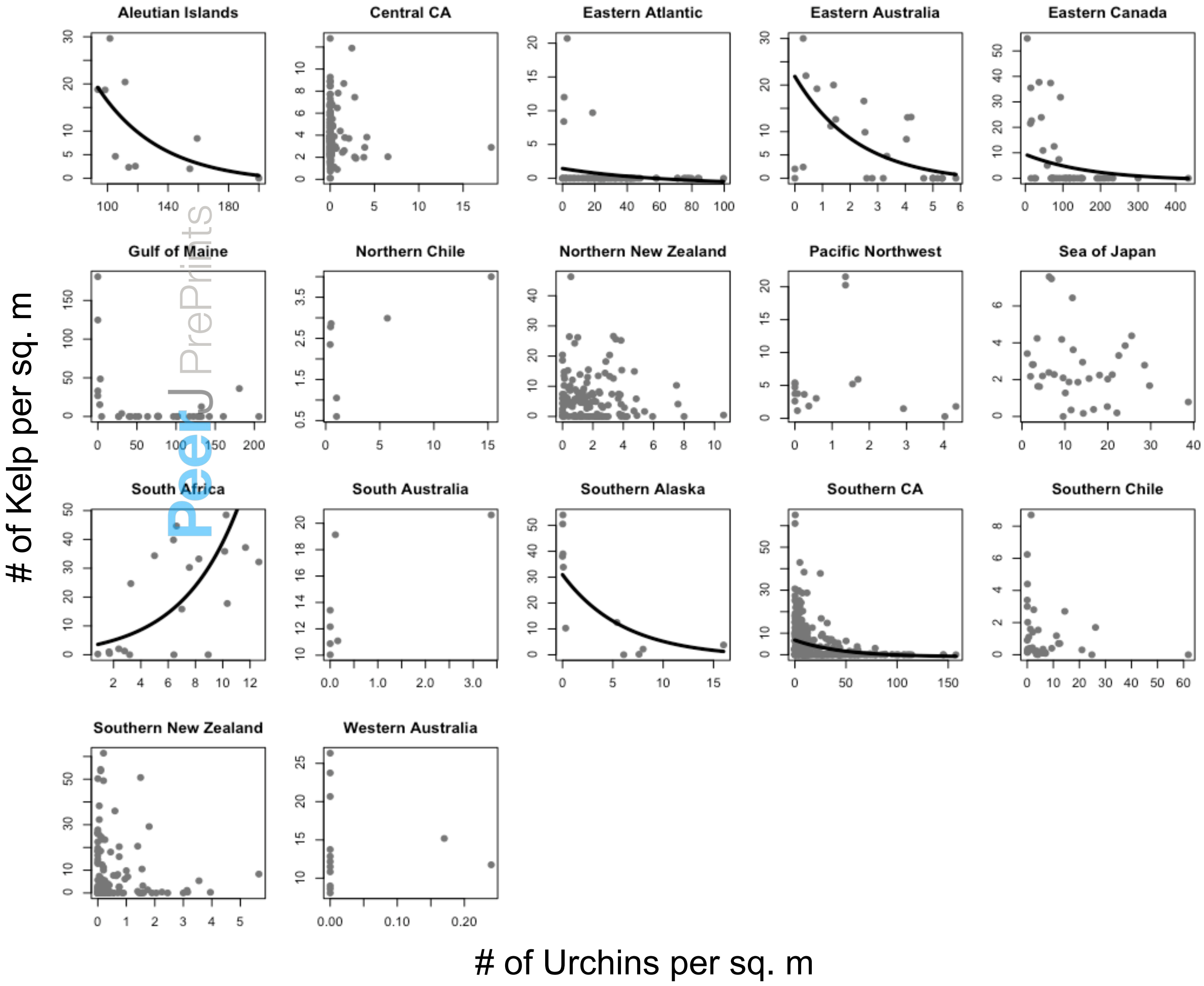
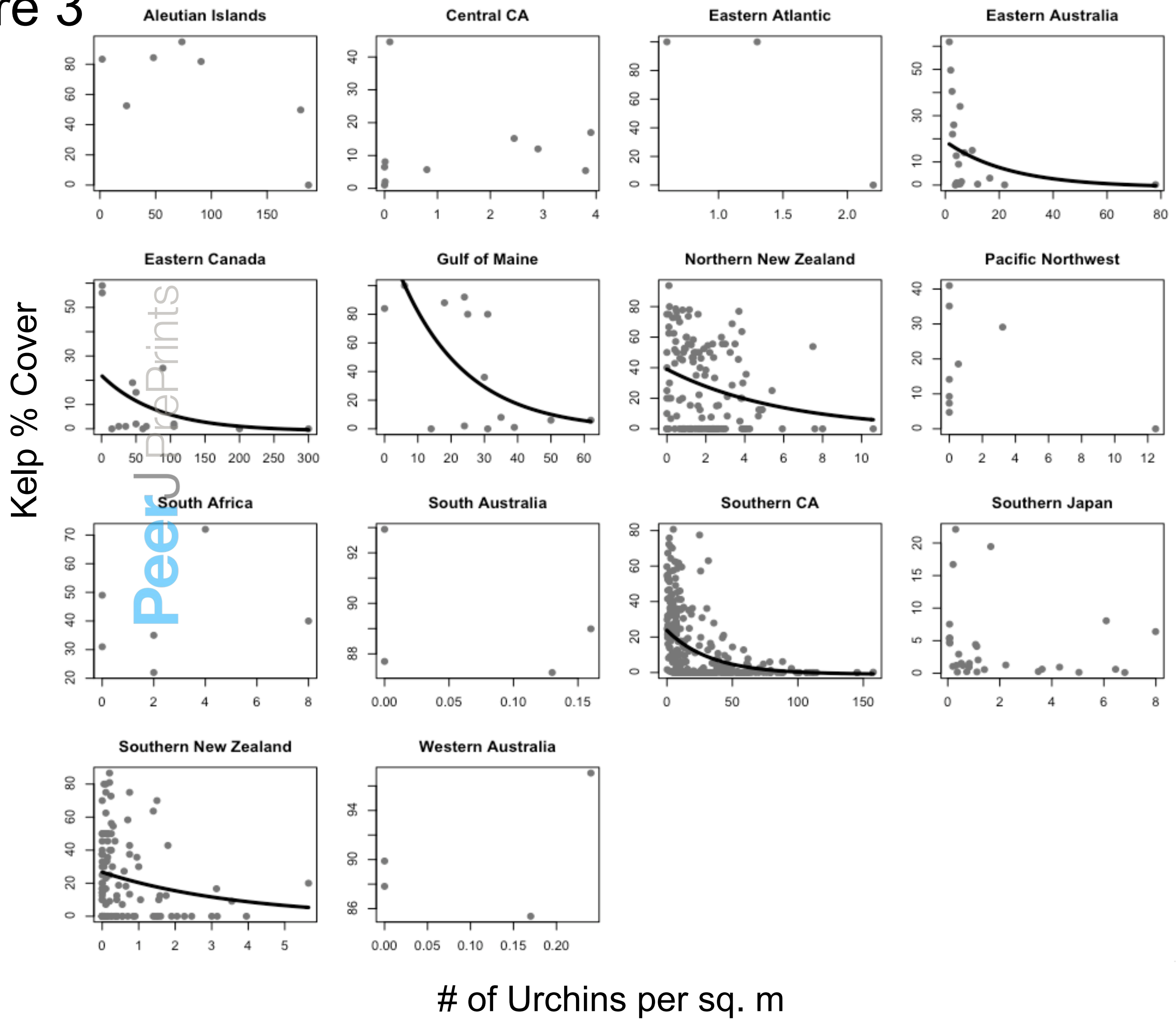
Figure 2



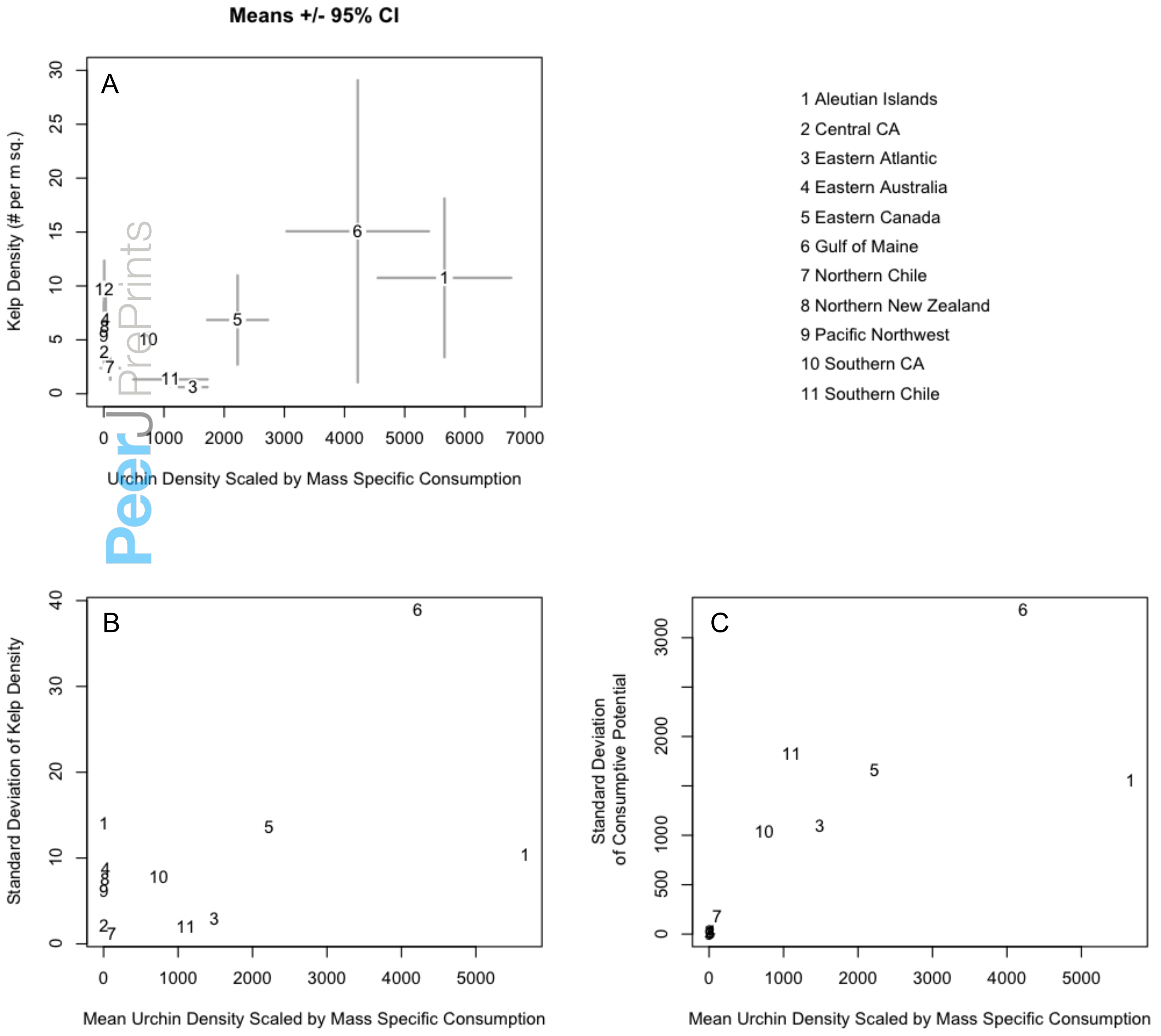
Aleutian Islands
Central CA
Eastern Atlantic
Eastern Australia
Eastern Canada
Gulf of Maine
Northern Chile
Northern New Zealand
Pacific Northwest
Sea of Japan
South Africa
South Australia
Southern Alaska
Southern CA
Southern Chile
Southern New Zealand
Western Australia
# of Kelp per sq. m
# of Urchins per sq. m

Figure 3



Kelp % Cover
# of Urchins per sq. m
Aleutian Islands
0 20 40 60 80
0 50 100 150
Central CA
0 10 20 30 40
0 1 2 3 4
Eastern Atlantic
0 20 40 60 80
1.0 1.5 2.0
Eastern Australia
0 10 30 50
0 20 40 60 80
Eastern Canada
0 10 30 50
0 50 100 150 200 250 300
Gulf of Maine
0 20 40 60 80
0 10 20 30 40 50 60
Northern New Zealand
0 20 40 60 80
0 2 4 6 8 10
Pacific Northwest
0 10 20 30 40
0 2 4 6 8 10 12
South Africa
20 30 40 50 60 70
0 2 4 6 8
South Australia
88 90 92
0.00 0.05 0.10 0.15
Southern CA
0 20 40 60 80
0 50 100 150
Southern Japan
0 5 10 15 20
0 2 4 6 8
Southern New Zealand
0 20 40 60 80
0 1 2 3 4 5
Western Australia
86 90 94
0.00 0.05 0.10 0.15 0.20

Figure 4



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