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Ecosystem features determine seagrass community response to sea otter foraging

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ABSTRACT

Comparing sea otter recovery in California (CA) and British Columbia (BC) reveals key ecosystem properties that shape top-down effects in seagrass communities. We review potential ecosystem drivers of sea otter foraging in CA and BC seagrass beds, including the role of coastline complexity and environmental stress on sea otter effects. In BC, we find greater species richness across seagrass trophic assemblages. Furthermore, *Cancer* spp. crabs, an important link in the seagrass trophic cascade observed in CA, are less common. Additionally, the more recent reintroduction of sea otters, more complex coastline, and reduced environmental stress in BC seagrass habitats supports the hypotheses that sea otter foraging pressure is currently reduced there. In order to manage the ecosystem features that lead to regional differences in top predator effects in seagrass communities, we review our findings, their spatial and temporal constraints, and present a social-ecological framework for future research.

1. Introduction

Seagrass ecosystem research has largely focused on bottom-up drivers of community dynamics and trophic interactions (Heck et al., 2000; Heck and Valentine, 2006). However, a growing body of research has demonstrated that predators can exert strong top down effects on seagrass and other coastal systems (Heithaus et al., 2012; Lewis and Anderson, 2012; Rosenblatt et al., 2013; Amundrud et al., 2015). Predator populations can contribute to the ecosystem services provided by seagrass (Atwood et al., 2015), and predator-induced trophic cascades can ameliorate the effects of environmental stress on seagrass (Hughes et al., 2013, 2016). Seagrass ecosystems provide a rich array of ecosystem services, including provision of food, sedimentation, nutrient cycling, protection of nearshore environments from storms, carbon flux and storage, and pathogen removal (Duarte et al., 2010; Barbier et al., 2011; Fourqurean et al., 2012; Greiner et al., 2013; Lamb et al., 2017; Macreadie et al., in press). Given the mounting evidence that predators and the ecosystem services provided by seagrass habitats are linked, we examine some of the factors that influence how a top predator affects seagrass communities. Specifically we use recovery of the sea otter (*Enhydra lutris*) to compare regional differences in the effects of sea otter foraging on seagrass communities in British Columbia (BC) and California (CA).

Our understanding of how sea otters can affect seagrass communities is recent (i.e., Hughes et al., 2013). Sea otters are best known for their effects in kelp communities; by preying on invertebrate herbivores, sea otters reduce grazing pressure and increase kelp biomass (Estes and Palmisano, 1974). Increased kelp in turn sequesters carbon (Wilmers et al., 2012), increases nearshore productivity (Duggins et al., 1989), reduces shoreline erosion and waterflow (Duggins, 1988), and improves habitat for abalone (*Haliotis kamtschatkana*; Lee et al., 2016), and rockfish (*Sebastes* spp.; Markel and Shurin, 2015). In fact, evidence connects the recovery of top predators with an array of diverse ecological effects across a variety of ecosystem types including intertidal, nearshore, and high latitude ocean ecosystems, in lake, and terrestrial ecosystems in tropical and boreal forests, deserts, and grasslands (reviewed in Terborgh et al., 2001, Terborgh and Estes, 2010, Ripple et al., 2014). However, in many systems where top predators have been restored, recovered or explicitly managed (see Maehr et al., 2001 for examples), the linkage between top-down effects and ecosystem effects

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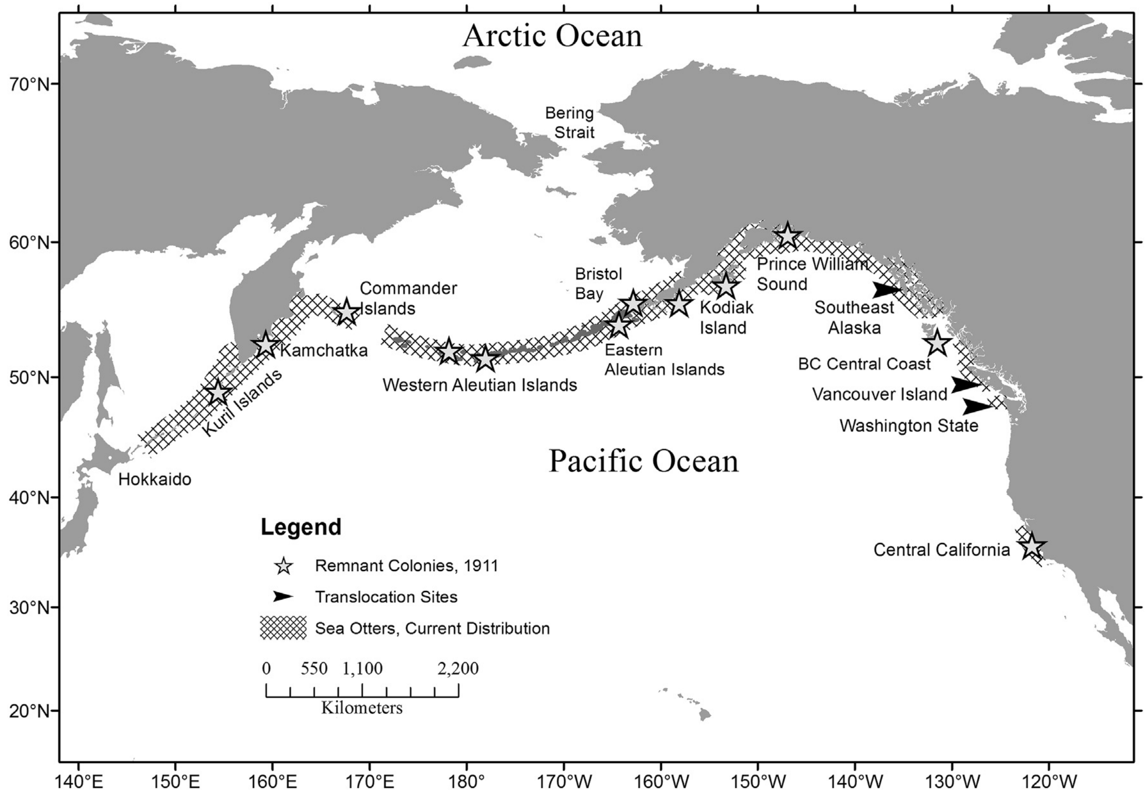

Fig. 1. Current distribution of sea otters from translocated populations and remnant colonies at the cessation of the fur trade (1911).

can be complex (Estes et al., 2011), context-specific (i.e., Foster and Schiel, 1988; Shears et al., 2008; Salomon et al., 2010), and often associated with socio-economic consequences (Marshall et al., 2016).

A growing literature on ecological resilience shows that ecosystems respond to change in a variety of sometimes non-linear ways, depending on the system's ability to resist and recover from change (Holling, 1973; Gunderson, 2000; Folke et al., 2004; Folke, 2006; Koch et al., 2009). Considering the features that confer resilience to an ecosystem (Unsworth et al., 2015), and observing the way in which an ecosystem resists and recovers from change, may help to explain the variable, nonlinear, and often context-dependent effects that predators have on ecosystems. This can be particularly important when top predators are reintroduced or recover from local extinction (Estes et al., 1989) and their effects result in changes to established socio-ecological systems.

Sea otters were extirpated from much of their range along the Pacific coast of North America during a maritime fur trade that lasted from the mid-1700s to the early 1900s. By the end of the fur trade there were likely 10 to 13 remnant groups that comprised fewer than 5000 animals (Riedman and Estes, 1990; Fig. 1). In central California, sea otters have increased slowly in abundance and distribution since the early 1930s, and in recent decades have colonized Elkhorn Slough, a tidal estuary in Monterey Bay. Their presence within Elkhorn Slough resulted in a trophic cascade in the seagrass community (Hughes et al., 2013, 2016). By consuming crabs, sea otters release mesograzers from predation pressure. Mesograzers clean epiphytes from seagrass, allowing it to thrive in eutrophic conditions (Hughes et al., 2013). The resulting positive effects on the extent and stability of seagrass habitats (Hughes et al., 2013) provides a clear example of how top predators can promote seagrass recovery and resilience (Unsworth et al., 2015). In British Columbia sea otters were successfully reintroduced in the early 1970s (Nichol et al., 2015). Although the effects of sea otters on BC kelp forests are well understood (Breen et al., 1982; Watson and Estes, 2011), their effects in soft sediment communities remain largely unstudied (but see Kvitek et al., 1988, Kvitek and Oliver, 1992, Kvitek et al., 1992 for their effects in California and Alaska).

Here, we investigate the effects of sea otter predation on the structure of seagrass communities on the Central Coast of BC, and compare these with those found in Elkhorn Slough, CA. In CA we restrict consideration to sea otters within Elkhorn Slough because it is currently the only area within CA that sea otters regularly utilize eelgrass habitat, and because this population is functionally discrete from the larger sea otter population occurring along the outer coast (Estes and Tinker, 2017). We compare these trophic patterns by considering features that influence seagrass community resilience (Unsworth et al., 2015) and highlight what we consider to be the most important ecosystem features for regional comparisons, including: nearshore habitat complexity, the spatial and temporal pattern of sea otter recovery, species diversity, species interactions, and bio-physical environmental stress (Table 1). We outline key hypotheses generated, based on review of our case study. To further this research, we identify the knowledge gaps that must be filled to manage both sea otters and seagrass communities and provide a general social-ecological framework that can be used to assess the impacts of top predators on ecosystem functions and services in nearshore communities.

2. Methods

2.1. Spatial shoreline complexity

We used ArcGIS (ESRI, 2010 Analysis Toolbox) to clip the North American shoreline base layer (Open Street Map, https://www.openstreetmap.org) to the latitudinal lines bounding the northern and southern extent of the sea otters' range in BC and CA. The length of coastline for each region was summed and then divided by the north-south distance in degrees of latitude for the respective region's sea otter range. For BC, we excluded the Strait of Georgia from the coastline length analysis as there are no historical record of sea otters using this area (Gregr et al., 2008). Coastline complexity was used as a first order metric to explore and approximate sea otter proximity to shelter and diverse habitat types (i.e., Gregr et al., 2008).

Table 1
Review of the key ecosystem features influencing the top down effects of sea otters in seagrass ecological systems, including data sources and methods/analyses to assess and quantify features. Hypotheses derived from reviewing and comparing British Columbia and California data are presented, as well as the research gaps and needs to address hypotheses and further research.

Ecosystem features	Data to quantify features	Methods and analyses	Hypotheses generated	Research gaps & data needs
Habitat complexity	Coastal habitat maps (seagrass, unvegetated soft sediment, subtidal kelp, rocky intertidal), time series of habitat data.	Mapping and change detection using remotely sensed imagery, surveys (low tide or subtidal), predictive habitat modeling.	Increased habitat complexity decreases the magnitude of sea otter ecosystem effects.	Regional gaps in spatial and temporal coverage of habitat data exist.
Top predator population trajectories	Sea otter censuses, observational foraging data, sea otter tagging programs.	Population assessments, movement and distribution models.	Sea otter diet changes with occupation time.	CA; well surveyed coastwide. BC; coastwide surveys ~5 years; focal annual surveys West Coast Vancouver Island (1987–present) & Central Coast (including seasonal surveys; 2013–present). Coastwide population surveys needed at time intervals to detect changes in population growth and distribution.
Predator-environment interactions	Sea otter distribution, movement and foraging observations by habitat type.	Long term surveys of otter densities, behaviour and foraging across habitat types. Change detection analyses using GIS-based spatiotemporal statistics.	Sea otter shift diets between habitats; clams and crabs dominate diets in protected soft sediments.	Coastwide aggregation of sea otter and seagrass spatial and temporal data.
Biodiversity	Community-level species richness and abundance.	In situ surveys of seagrass parameters and community constituents. Analysis of time series and spatial dynamics.	Increased seagrass trophic assemblage diversity mitigates top-down predator effects. Increased functional redundancy promotes weak species interactions.	Intensive research “hot spots” exist regionally. Additional geographic sampling needed to cover spatial extent of sea otters. Standardized metrics across sites are needed.
Species interactions	Observational and experimental trends in seagrass-associated populations and communities.	Analysis of trophic trends & feeding ecology to determine interaction strengths and direction. Time series analysis.	Weak species interactions decrease the strength of trophic cascades, but strong species interactions may strengthen them.	Comparative experimental designs for manipulative and process-oriented studies. Modeling approaches for coastwide comparisons.
Bio-physical features of supporting ecosystem: water quality & climate	Water column and atmospheric monitoring data.	Analysis of long term trends, and correlations with seagrass parameters, including resilience metrics.	Less stressful conditions increase seagrass resilience to disturbance.	Coastwide comparisons, long term datasets needed.

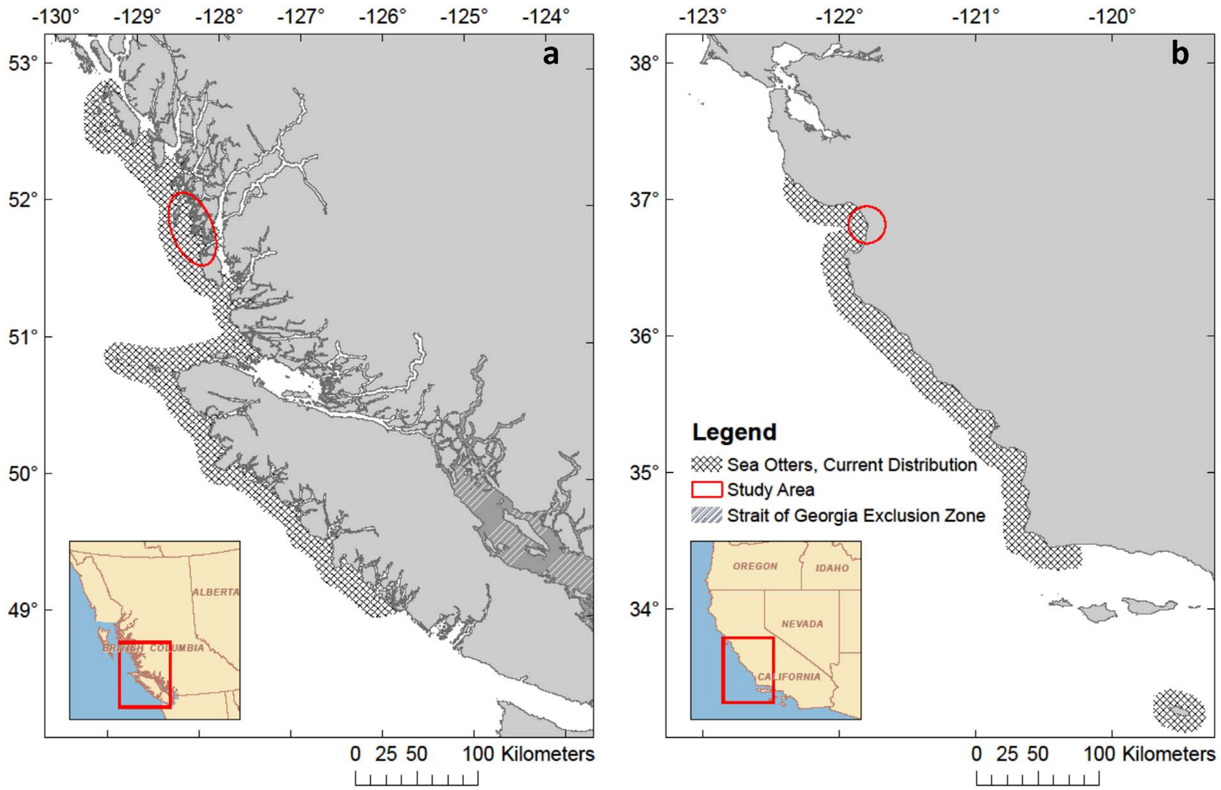

Fig. 2. Coastline comparisons between British Columbia (BC - panel a) and California (CA - panel b) show greater shoreline complexity in BC than CA, given roughly equivalent N-S distance (~5° latitude). Hashed polygons indicate sea otter range on Central Coast of BC and CA. Red ovals show study areas: Central Coast, BC and Elkhorn Slough, CA. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

2.2. Seagrass community richness, structure and species interactions

Seagrass (*Zostera marina*) community data were collected in 2016 (July/August) on the Central Coast of BC (Fig. 2a) at four regions: Calvert, occupied by sea otters since 2014; Triquet, occupied by sea otters since 2011, McMullins, occupied by sea otters since 1996, and the Goose Group, occupied by sea otters since the early 1980s (n = 1–2 meadows per region). Within each seagrass meadow, crabs were counted along six 60 m^2 transects (30 m long, with survey counts within a 2 m swath; 1 m on either side of the transect line) using SCUBA. Crab counts were summed over all transects and seagrass meadows for an estimate of relative abundance and species richness across regions. The biomass of mesograzers, algal epiphytes, and seagrass was measured from shoot-level collections (n = 4 per transect, every 10 m), and scaled spatially based on density counts (n = 7 per transect, 0.25 m by 0.25 m quadrats every 5 m). Seagrass blades were scraped of epiphytes and mesograzers, and then each trophic group was sorted, and dried at 60 °C for 48 h. The methods and metrics used in CA were comparable (see Hughes et al., 2013). Briefly, in CA seagrass density and collections were also made along transect lines (4 seagrass beds in Elkhorn Slough, 100 m transect per bed, 0.50 m by 0.50 m quadrat for density counts, 8 quadrats spaced every 10–12 m, 5 shoots collected per quadrat for seagrass, epiphyte and grazer biomass). In CA, crab densities were assessed using CPUE data from crab traps (1 trap per site, CPUE based on average crab biomass per trap soak time, repeated daily). This differs from the observational SCUBA surveys used to measure crab abundance in BC. Fish richness was also compared (CA vs. BC) using standardized beach seining at shallow seagrass sites in 2016 [beach seine net dimensions: 11 m or 22 m in length, 3 m centre with 14.5 m bridles, 4 mm stretch mesh, sampling area average size of 230 m^2 +/− 88 m^2, respectively (CA): 10 m in length, 6.35 cm stretch mesh, sampled over 200 m^2]. Beach seining is a common method used for community-level assessments of nearshore fish in shallow waters with low visibility, where visual surveys are difficult (e.g. Negelkerken et al., 2001; Pihl et al., 2006). To test for differences among occupation times for crab abundance, mesograzer biomass, algal epiphyte biomass, and seagrass biomass, we used a non-parametric Kruskal-Wallis test. Dunn's tests were used post-hoc for multiple comparisons between occupation times.

In BC, sea otter foraging observations were conducted year-round from 2014 to 2017, across areas that were recently occupied (Calvert and Triquet) and longer occupied (McMullins and Goose Group) by sea otters. Observations were made from shore with consistent methods and observers among years. Near-daily observation were made by four observers (January–February, July–August) in all study years. Observations were spatially coupled with seagrass community data collections. Sea otters dive to locate prey, but consume it at the surface. We used a Questar 50-80 × spotting scope, set up on shore, to observe prey items brought to the surface by foraging sea otters (i.e., Estes et al., 1982; Bodkin et al., 2001; Tinker et al., 2008) that had access to both seagrass and open coast habitats (both habitats within 1000 m of foraging otters). An individual sea otter was observed for successive foraging dives, referred to as a foraging bout. We identified all prey items, and recorded dive and surface durations, and used these data to estimate the proportion each prey type contributed to the diet in terms of consumed biomass. A Monte Carlo algorithm was used to account for uncertainties and biases associated with unidentified prey (see Tinker et al., 2012). These methods are identical to those used in previous analyses of sea otter diets (e.g. Tinker et al., 2008, 2012) and correspond with protocol in Hughes et al. (2013), except that we used a space-for-time substitution (Pickett, 1989) to approximate the ~13 year collection of foraging data in Elkhorn Slough. To test for differences in prey composition of sea otter diets between 1) CA and BC, and 2) among the four sites in BC, we used a Pearson's Chi-squared test (R Core Team, 2017), where Pearson residuals examined the probability of consuming specific prey items more or less than expected.

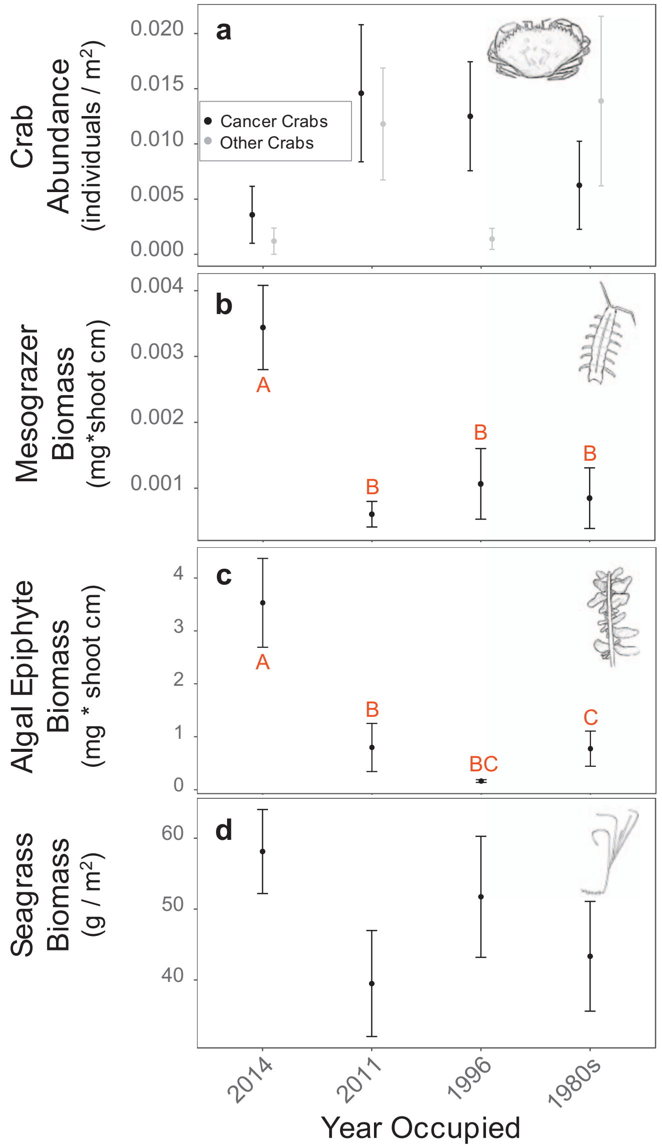

Fig. 3. Community structure of four seagrass trophic assemblages on the Central Coast, BC at regions varying in sea otter occupation time from recent (Calvert, 2014 and Triquet, 2011) to long-occupied (McMullins, 1996 and Goose Group, 1980s). a) Crab abundance per region (from visual surveys, n = 43 transects), b) mesograzer biomass per shoot (mean by region), c) epiphyte biomass (mean per region), and d) seagrass biomass (mean per area by region), were collected in in 2016. The biomass of mesograzers, epiphytes, and seagrass (b–d) were estimated on a seagrass-blade level at each occupation time (Calvert: n = 83; Triquet: n = 36; McMullins: n = 35; and Goose Group: n = 35). Error bars represent standard errors and red letters represent significant differences among occupation time. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

2.3. *Environmental stressors and seagrass stability*

We assessed the latitudinal relationship between environmental stressors to seagrass and the mean annual change in seagrass cover, a metric of seagrass stability, across the sea otter range. To determine the linear relationship between stressors and latitude we used a principal components analysis of three seagrass stressors: nutrients (mg/L nitrate), chlorophyll *a* (μg/L Chl *a*), and temperature (degrees Celsius) (Supplementary Information - SI). We compiled data from monitoring stations (n = 23) located within six Pacific coast estuaries from San Diego, CA to Kachemak Bay, AK (SI). Data used were from the NERR SWMP database (http://cdmo.baruch.sc.edu). The temperature data were collected every 15 min, and nitrate and chl *a* was collected monthly. We used data from summer months only (June to August) for 2009 and 2010 to focus on the peak seagrass biomass. Because of multicollinearity among stressors (SI), we analyzed their aggregative latitudinal trends using ordination (i.e., PCA; Graham, 2003). PCA was run using the *prcomp* function in R (R Core Team, 2017) using the mean nitrate and chl *a* values, and the 90th percentile temperature (an indicator of high temperatures) for each estuary. We ran a linear regression between latitude and the first principal component scores of the three stressors.

To determine seagrass stability, data from multiple sources and sites across the seagrass-sea otter latitudinal range were analyzed. We use directional change in percent cover as a metric of relative seagrass stability to capture both negative and positive responses to stress and/or disturbance relative to long-term means. We used the following criteria for inclusion in this dataset: 1) measurements of annual change of bed extent (hectares), 2) a minimum of three years of data, and 3) seagrass extent > 1 ha. Eight sites across the targeted latitudinal range met these criteria, including Funter Bay, AK; Crab Bay, AK; Izembeck Lagoon, AK; Puget Sound, WA; Elkhorn Slough, CA; Morro Bay, CA; Tomales Bay, CA; and San Francisco Bay, CA (Waycott et al., 2009, Hughes et al., 2013; National Marine Fisheries Service 2008; Merkel, 2010; Morro Bay National Estuary Program, 2013). Stability was defined as the mean absolute (either decreasing or increasing) percentage change for each site, under the assumption that stable seagrass beds are those without high fluctuations (negative or positive) in cover across annual time scales. We ran a linear regression between latitude and the mean annual change across all sites.

3. Results

3.1. *Shoreline and habitat complexity*

The linear coastline length of the sea otter range in CA and BC are similar [CA population: ~33.2°N – 37.2°N (Tinker and Hatfield, 2016), BC population 49.1°N – 52.8°N (Nichol et al., 2015)]. However, due to shoreline complexity (Fig. 2), the BC coast, over a similar latitudinal range, is ~10 × longer than the CA coastline, with 4738 linear km of coastline per degree of latitude (BC) compared with 430 km per degree of latitude (CA). Comparative habitat maps are not currently available for BC and CA, but this first order approximation of shoreline complexity suggests that BC's more complex shoreline provides sea otters with access to a greater diversity of habitats, including sheltered waters. For example, in BC, seagrass and kelp forests are often proximately located, even intermixed (M.H.L. unpublished data), whereas on the CA coast, seagrass is generally limited to protected estuaries, and kelp is spatially separated on exposed rocky coasts. As sea otters forage over both protected and exposed coastal habitats, the proximity and configuration of habitats should affect sea otter distribution, carrying capacity, seasonal movement and range expansion (Gregr et al., 2008). In CA, almost all sea otters found within Elkhorn Slough foraged exclusively within the estuary, and in a concurrent radio tagging study (USGS unpublished data) few tagged otters within the slough travelled to the rocky outer coast during 3 years of monitoring (one tagged male otter left the slough briefly, but returned). By contrast, in BC, individual sea otters frequently dive over both seagrass and exposed rocky habitats within a single foraging bout (EUR personal observations). To the best of our knowledge there are no groups of sea otters that exclusively use seagrass habitats on the BC Central Coast.

3.2. *Seagrass biodiversity, community structure and predatory interactions*

In BC, at recently-occupied sites (Calvert, Triquet), there was little evidence for top-down trophic effects via sea otter predation on crabs (Fig. 3a). Calvert (occupied 2014) had the lowest crab abundance, whereas Triquet (occupied 2011) had the highest, but no overall differences were observed among sites/occupation times (Fig. 3a, K–W

Table 2

Comparative species richness (species number) between CA and BC for seagrass trophic assemblages. Epiphytes and mesograzers: CA = plot-level metrics (2012, n = number of quadrats), BC = blade-level metrics (2016, all blades collections per site, n = sites). Crabs: CA = CPUE by shrimp pot (2016, n = number of pots), BC = site-level total richness using visual dive surveys (2016, all transects per site, n = sites). Fish: CA and BC = standardized beach seining (n = number of sites).

Trophic group	Richness by area	
	California (CA)	British Columbia (BC)
Epiphytes	4 (n = 32)	4 (n = 9)
Mesograzers	1.69 ± 0.70 (n = 32)	3.91 ± 2.12 (n = 9)
Crabs	1.38 ± 1.08 (n = 94)	3.5 ± 1.19 (n = 7)
Fish	3 ± 2 (n = 3)	11.3 ± 1.5 (n = 3)

test, $p > 0.05$). Seagrass biomass, epiphyte biomass, and mesograzer biomass were all positively associated (Fig. 3a–d), but only epiphytes (K-W test $p = 9.19E^{-14}$) and mesograzers (K-W test, $p = 2.39E^{-15}$) were different between sites/occupation times. While patterns indicate a decline in *Cancer* spp. crab abundance across the sites with longer sea otter occupation times (McMullins and Goose Group), seagrass, algal epiphyte and mesograzer biomass trends did not support a cascade mechanistically (Fig. 3).

Similar to the Elkhorn Slough seagrass community, epiphyte biomass was dominated by diatoms and the red alga *Smithora naiadum*, and mesograzers consistently included *Idotea* spp., gammarid amphipods, *Lacuna* spp. snails and few *Phyllaplysia taylori*. *Cancer* spp. and kelp crabs dominated the crab assemblage. Total species richness across all trophic groups, except epiphytes, differed between BC and CA (Table 2: mesograzer, crab and fish assemblages were more speciose in BC than CA).

Sea otter diets along the Central Coast of BC differed from sea otter diets in Elkhorn Slough, CA ($\chi^2 = 75.37$, df = 5, $P < 0.001$). In BC, *Cancer* crab consumption was lower than expected (5% of diet), whereas sea urchin consumption was higher than expected (44% of diet) when compared with sea otter diets in CA (42% *Cancer* crabs, 0% urchins; Fig. 4a, SI). Within BC, prey consumption varied with sea otter occupation time ($\chi^2 = 198.4$, df = 15, $P < 0.001$). Sea otter diets at recently occupied sites had higher than expected sea urchin consumption (74% of diet at Calvert, compared with < 20% of diet at McMullins and Goose Group, Fig. 4b–e, SI). Clam consumption was higher than expected at the McMullins (48%; Fig. 4d, SI), but lower than expected at Goose Group (11%, Fig. 4e & SI). At the longest-occupied site (Goose Group), sea otter diets were the most diversified among prey (Fig. 4e, SI). This contrasts with findings from Hughes et al. (2013), where sea otter diet in Elkhorn Slough from 1999 to 2012 was composed of 43% *Cancer* spp. crabs, 39% clams, and 18% other prey items during a period of rapid population increase (Fig. 4a). In subsequent years, sea otter diet in Elkhorn Slough has shifted to predominantly clams and smaller crabs, likely because larger *Cancer* crabs have become depleted (USGS, unpublished data).

3.3. *Environmental stressors and seagrass stability*

Along the Pacific coast of North America, the strength of aggregative environmental drivers/stressors increased from north to south ($P = 0.003$, $R^2 = 0.915$, df = 4; Fig. 5a). PC1 represented 87% of the variation among the three stressors (temperature, nutrients and chlorophyll *a*). Similarly, annual percent change in seagrass, our measure of bed stability, increased along this same latitudinal gradient ($P = 0.004$, Rsq = 0.778, df = 6; Fig. 5b), indicating that seagrass beds were less stable in southern latitudes which co-varied with increasing environmental stress.

4. Discussion

This is the first study to examine how the effects of sea otter predation differ among seagrass systems. Our review, based on available data from BC and CA, provides the foundation for testing new hypotheses about sea otter effects on seagrass ecosystems (Table 1), and for further discussion and generalization about the key seagrass ecosystem features regulating top predator effects in coastal systems.

In BC, the richness of seagrass mesograzers, crabs and fish assemblages was greater than those observed in Elkhorn Slough (Table 2). In CA, *Cancer* spp. crabs (Hughes et al., 2013), were the dominant sea otter prey item (43% of diet; Fig. 3a) whereas in BC, clams (28% diet) and urchins (44% diet; Fig. 3a) made up most of the sea otter diet. Sea otters in our CA sample were limited to the prey available in Elkhorn Slough and did not have easy access to the rocky outer coast, whereas BC otters had ready access to multiple habitats (we note that diets of sea otters on the outer coast of CA are very different from those measured in Elkhorn Slough; see Tinker et al., 2008, 2012). Together, differences in species richness and their effect on sea otter diet, may explain why the trophic cascade brought about by sea otters eating crabs in seagrass beds in CA (Hughes et al., 2013) has not been observed in the community structure of the BC seagrass habitats (Fig. 3).

The aggregate latitudinal trends in water quality and temperature suggest that seagrass beds on the Central Coast of BC are subject to lower stress compared to those in CA (Fig. 5). In addition, both habitat complexity and sea otter occupation times differed between BC and CA. Coastline complexity, a first order approximation of habitat diversity, was greater in BC (Fig. 2). These differences likely mediate how sea otter foraging affects seagrass communities. Longer occupation time in CA likely means reduced prey abundance; a factor that could be mediated in BC by the availability of greater habitat diversity.

4.1. *Biodiversity and food web structure*

Based on studies in other seagrass ecosystems, increased biodiversity, especially among macrophytes, invertebrate grazers, crab and fish, generally increases resiliency (Tilman, 1996; Yachi and Loreau, 1998; Duffy, 2006; Duffy et al., 2015; Stachowicz et al., 2007). Following the generalized view that diversity begets resiliency, we suggest that increasing assemblage diversity could also mitigate the top-down changes induced by sea otter predation (Table 1; Hypotheses). We predict that the greater species diversity seen in BC seagrass beds might reduce the effects of sea otter foraging on seagrass community structure and function (Table 2, Fig. 3).

Biodiversity also influences food web structure (Worm and Duffy, 2003; Thompson et al., 2012). If diversity increases functional redundancy, species are more likely to have weak interaction strengths which should stabilize the system (Duffy et al., 2007; Heck and Valentine, 2006, Rooney and McCann, 2012). Whereas, if increased diversity reduces species evenness (i.e., the relatively even distribution of species abundances), this may favor interactions between more abundant species and increase the number of strongly interacting species. The role of both strong and weak species interactions on predator-induced trophic cascades in seagrass systems should be examined mechanistically (Table 1; Research gaps), building on the comparative results of this study (Figs. 3 and 4).

4.2. *Bio-physical drivers of change*

Bottom-up drivers of seagrass communities such as temperature, salinity, light, alkalinity/pH, and nutrients (Orth et al., 2006; Short and Neckles, 1999; Palacios and Zimmerman, 2007) can act as stressors, or press disturbances when they limit seagrass productivity (Waycott et al., 2009). When these factors collectively, or independently, exert strong bottom-up control on seagrass production they can reduce the resilience of seagrass communities.

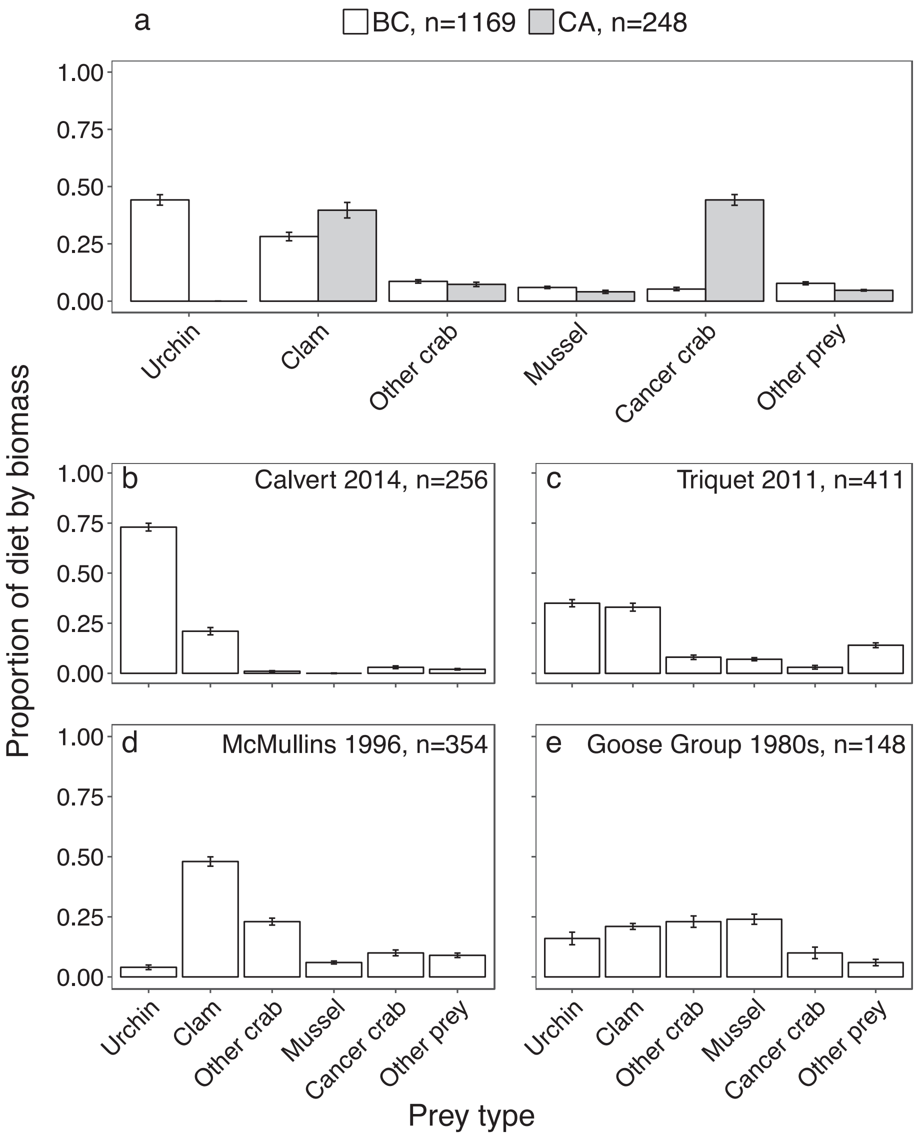

Fig. 4. Prey items composing > 5% of sea otter diets in areas spatially coupled with seagrass community data collections are shown with white bars for the Central Coast, BC (a) and grey bars for Elkhorn Slough, CA (a). Panels b–e show Central Coast, BC sea otter diet at sites occupied at: Calvert, occupied in 2014 (b); Triquet, occupied in 2011 (c); McMullins, occupied 1996 (d); and Goose Group, occupied early 1980s (e).

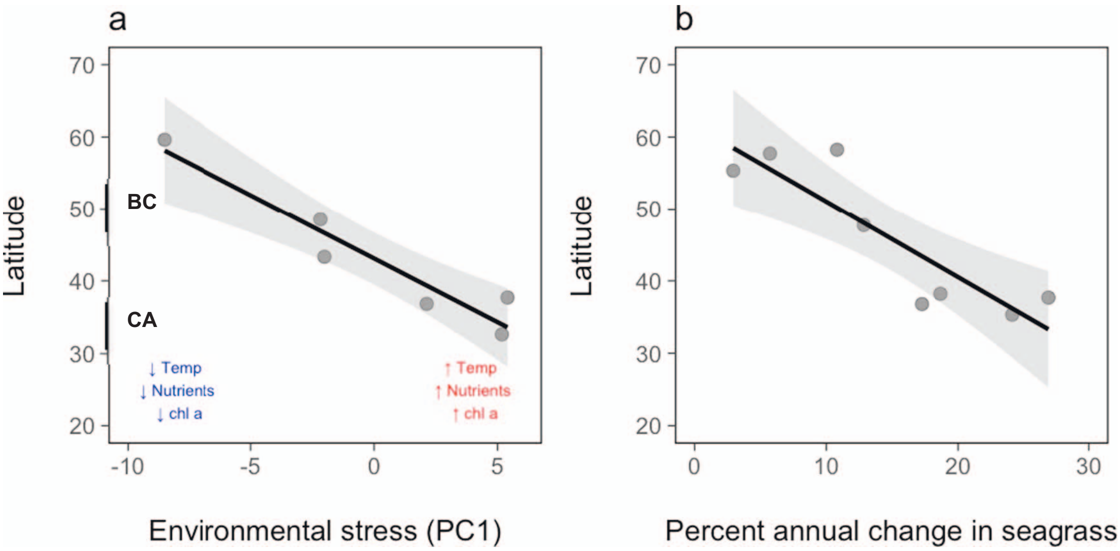

Fig. 5. a) Latitudinal trends in aggregative seagrass environmental stressors: temperature, nitrate (NO_3), and chlorophyll *a* (an indicator of eutrophication). PC1 represents 87% of the variation from the Principal Components Analysis (PCA) for these stressors. b) Percent annual change in seagrass cover with latitude. Latitudinal data is associated with monitoring sites and studies located along the Pacific Coast of North America (SI). Grey areas represent 95% CI. Black lines on y-axis indicate current latitudinal range of BC and CA sea otter populations. Error bars represent standard deviations.

Along the Pacific Coast of North America, we found that the strength of aggregative bottom-up drivers increased from north to south (Fig. 5a). The annual change in seagrass cover, one metric of seagrass resilience, follows a similar trend, suggesting a correlative relationship between increased environmental stress and reduced resilience (Fig. 5b). In Elkhorn Slough nutrient loading from agricultural sources created eutrophic conditions generally harmful to seagrass beds, that were alleviated by the strong top-down effects of otters (Hughes et al., 2013). Globally, terrestrial nutrients are known as a source of stress to seagrass communities (Orth et al., 2006; Burkholder et al., 2007), including rocky intertidal *Phyllospadix* spp. surfgrass communities (Honig et al., 2017) and estuarine fish communities (Greene et al., 2014). However, the role of top predators in mitigating the effect of environmental stressors on seagrass communities needs more comparative investigation (Table 1; Research gaps).

4.3. Predator-habitat interaction in time and space

Seagrass bed stability, and other important components of resilience, are relative to both the temporal and spatial extent of the data collected. Our assessment of seagrass stability and key ecosystem features, is constrained by the length of the study, and absence of a clear baseline or reference point. Shelton et al. (2016) examined 40 year trends in seagrass stability in Puget Sound, Washington located between our two study regions and found that seagrass beds exhibit stability at the scale of whole estuaries, but with substantial small scale variation (0–1 km), suggesting that longitudinal datasets will be necessary to tease apart long term bottom-up induced trends from those top-down effects caused by recovering predators like the sea otter (Table 1; Research gaps).

Sea otters first moved into Elkhorn Slough in 1984 (Kvitek et al., 1988); however, through the 1990s the Slough was primarily used seasonally by transient male otters. By the early 2000s, a resident population of territorial males and females foraged year-round on benthic invertebrate communities in the soft sediment and eelgrass communities within the Slough (Maldini et al., 2010; Estes and Tinker, 2017). On the Central Coast of BC, sea otter recolonization dynamics were approximated using a space-for-time substitution; transient males occurred at Calvert (in 2014), and resident groups occurred at Triquet (population increasing rapidly since 2011), the McMullins (since 1996), and Goose Group (since 1980s; Nichol et al., 2015). In BC, sea otters move between exposed and sheltered waters seasonally at both recently and long-occupied sites, and are frequently observed foraging between both kelp forests and adjacent seagrass meadows (E.U.R. unpublished data). In CA, Elkhorn Slough otters forage exclusively within the estuary.

In CA, sea otters, have expanded their range and increased in abundance since the discovery of a remnant population in 1938 (Bolin, 1938). The CA population appears to be nearing carrying capacity over much of its current range, at ~3000 individuals (Tinker and Hatfield, 2016), with range expansion at the north and south ends of the range currently being curtailed by shark-bite mortality (Tinker et al., 2015; Fig. 2b). In BC, sea otters reintroduced to the West Coast of Vancouver Island from 1969 to 1972 expanded to the Central Coast of BC in the early 1980s (Nichol et al., 2015; Fig. 2a). Along the west coast of Vancouver Island, where sea otters were reintroduced, some areas appear to be at carrying capacity (Nichol et al., 2015) whereas in other areas, sea otters continue to increase in abundance and expand their distribution. Likewise on the Central Coast of BC, some areas, long-occupied by sea otters have undergone few recent changes in abundance, but the overall abundance and range of sea otters continues to increase (Nichol et al., 2015). We posit that the recent occupation times of sea otters and the more complex coastline (Fig. 2), which likely increases habitat and species diversity along the BC coast, may mitigate the top-down effects of sea otter foraging in soft sediment habitats as compared to those seen in Elkhorn Slough, CA (Table 1; hypotheses).

Our observations suggest that in BC, diffuse foraging patterns, and the shift in feeding between adjacent kelp forests and seagrass beds, may reduce the per area predation in nearshore habitats compared to CA (Fig. 4a). Interpretation of space-for-time study designs are constrained by differences in the characteristics of sites used to approximate temporal change (e.g., Johnson and Miyanishi, 2008). We limited our analysis to seagrass sites with large, continuous seagrass meadows (~2000 m^2–500,000 m^2). Going forward, habitat mapping and continued observational surveys of seagrass parameters are necessary (Table 1; Research gaps) to incorporate site-level spatial covariates in analyses.

4.4. Integrated research on top predators and seagrass ecosystem features; a framework for future research

The results of our study suggest that differences in ecosystem attributes may determine how resilient seagrass communities are to disturbance and stress, and govern how sea otters affect seagrass ecosystems. Here, we propose a Social-Ecological System (SES) conceptual framework to guide the direction of future work, and contribute to successful habitat and wildlife management. This model, adapted from Collins et al. (2010), emphasizes ecological resilience by linking social and ecological systems via disturbance. Although we apply this framework to the sea otter-seagrass case study (Fig. 6), the model can be generalized to any hypothesis-driven research examining seagrass communities across different types of human-environment interactions (Kenworthy et al., 2006) and can be tailored to examine questions on any scale. Below, we provide examples, stemming from our comparative review, that illustrate the linkages between seagrass function, ecosystem services and human, social systems.

Our results suggest that top predator effects in seagrass systems will likely favor certain seagrass ecosystem services over others. In CA, trophic effects brought about by predation on crabs have likely enhanced seagrass productivity and linked ecosystem services, such as provision of fish and crab habitat (Fig. 6). In BC, sea otters consume a greater proportion of clams compared to crabs (Fig. 4a) especially at seagrass sites long-occupied by otters (Fig. 4b). Digging by sea otters may affect seagrass ecosystem function via bioturbation. Depending on the severity of this disturbance there may be positive feedbacks on the carbon storage services delivered by seagrass communities with changes to benthic metabolism, carbon burial and sediment capture. As ecosystem services serve as a common currency between social and ecological systems (Fig. 6), variability in their outcomes can impact decision-making processes in coupled social and ecological systems. For instance, sea otter populations in seagrass beds may be managed for continued growth if their impacts contribute to seagrass ecosystem services prioritized by local and regional needs.

Sea otters may also have indirect effects on seagrass community structure (Fig. 6). When otters eat clams and drop shells to the sea floor, the shells can provide substrate that promotes seaweed growth, and enhances fish habitat (Fig. 6). Fish also feed on seagrass-associated mesograzers (Hughes et al., 2016, Olson, 2017), introducing potential habitat-mediated trophic effects (Fig. 6). Furthermore, the clam pits dug by otters expose small clam recruits that are then fed on by sea stars and crabs (Kvitek et al., 1992). The disturbance created as sea otters dig for clams may have both positive and negative effects on seagrass communities, depending on the magnitude of disturbance. Studies show that seagrass plants respond to small scale disturbance caused by recreational clam harvesters by increasing reproductive effort rather than vegetative growth (Alexandre et al., 2005) and are resilient to the small-scale harvest of rhizomes (Cullis-Suzuki et al., 2015). The thresholds at which digging by sea otters negatively affects seagrass communities has not been studied, but is important for understanding how seagrass ecosystem services, including both provision of food and carbon storage, are affected by sea otters and linked to social systems (Fig. 6).

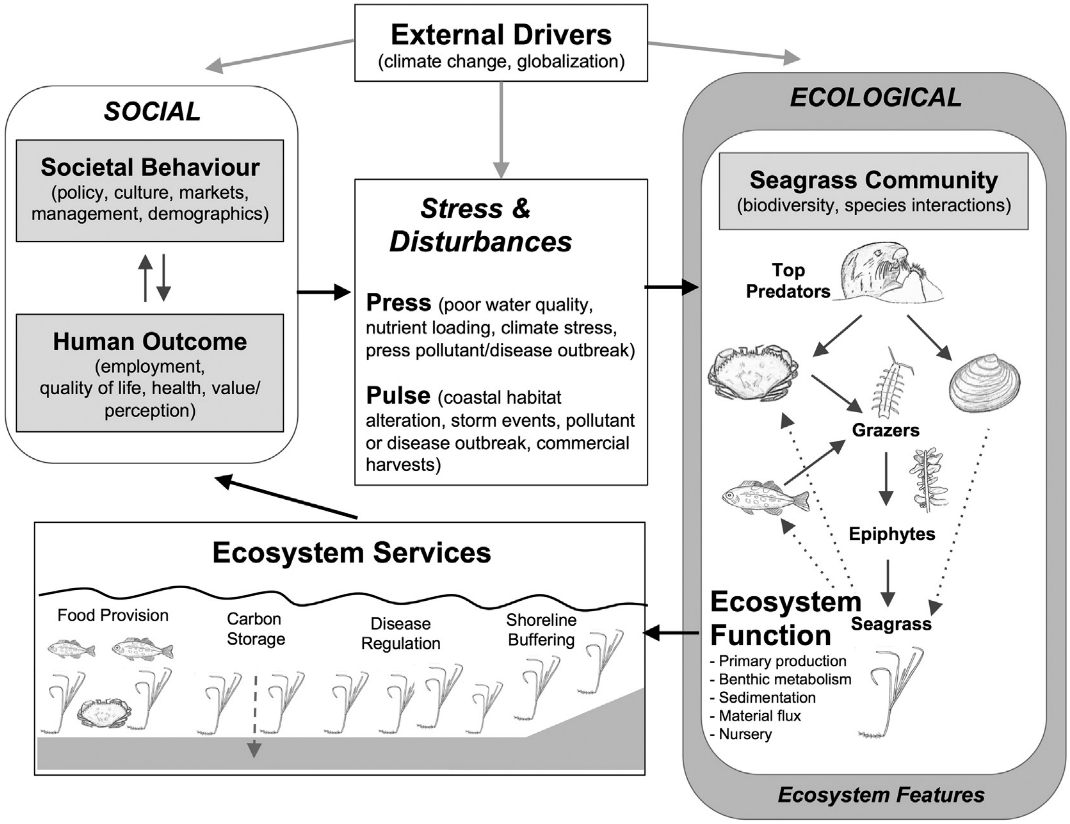

Fig. 6. Social-Ecological Systems (SES) conceptual model. Press-pulse disturbances (press = high frequency events, inclusive of stress, pulse = lower frequency, high magnitude events) affect the ecological system. The seagrass community's ability to resist and recover from disturbance is buffered by the ecosystem's inherent and supportive features (supporting bio-physical/ecosystem and seagrass properties), which affect ecosystem function. For ecological interactions, the solid lines represents direct interactions, dotted lines indirect interactions/ feedbacks. Seagrass ecosystem functions provide ecosystem services to humans, which are linked to adjoining social systems, including both human outcomes (e.g., employment and health) and human behavior (e.g., policy, markets and culture). External drivers influence all system components.
Adapted from Collins et al. (2010).

In CA, state-level policy strongly supports climate change initiatives (Bedsworth and Hanak, 2013), which may include the carbon sequestration provided by seagrass. Likewise, seagrass ecosystem services such as the reduction of human bacterial pathogens and contamination (Lamb et al., 2017) are well paired with management objectives in regions with high human population densities such as CA. The local CA scenario, with sea otters enhancing seagrass, presents a good match between ecosystem service and policy/management. In BC, trade-offs in ecosystem services may arise from diverse human values across different coastal communities. BC seagrass meadows enhance crab and fish abundance, and nursery habitat (Olson, 2017), providing ecosystem services in a region where sea otters, and their ecosystem interactions, are highly valued culturally (Salomon et al., 2014). Here, governmental policy and management decisions, at different spatial scales, should include mechanisms that recognize and incorporate differences in human values between communities that differ in their perceived benefits from coastal ecosystems. In sum, a social-ecological system framework allows us to frame testable research about top predator effects and ask questions about how seagrass ecosystem services influence policy, management and markets, and affect human and social well-being, using an interdisciplinary approach.

The results of our study suggest that the effects of sea otters on seagrass communities and the ecosystem services they deliver will be governed by regional environmental, geographic and ecological features. We further propose that these regional and local differences need to be considered when making management or policy decisions about tightly linked social and ecological systems. Use of this coupled approach, together with future research that addresses key knowledge gaps, presents an optimistic outlook, for both predators, and the coastal ecosystems they inhabit.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marpolbul.2017.09.047.

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