# Ecosystem features determine seagrass community response to sea otter foraging

Margot Hessing-Lewis[a,*], Erin U. Rechsteiner[a,b], Brent B. Hughes[c,d], M. Tim Tinker[e], Zachary L. Monteith[a], Angeleen M. Olson[a], Matthew Morgan Henderson[a], Jane C. Watson[f]

[a] Hakai Institute, PO Box 309, Heriot Bay, BC V0P 1H0, Canada
[b] Applied Conservation Science Lab, University of Victoria, PO Box 3060 STN CSC, Victoria, BC V8W 3R4, Canada
[c] Institute of Marine Science, University of California Santa Cruz, 115 McAllister Way, Santa Cruz, CA 95060, USA
[d] Division of Marine Science and Conservation, Nicholas School of the Environment, Duke University, Beaufort, NC 28516, USA
[e] U.S. Geological Survey, Western Ecological Research Center, Long Marine Laboratory, 115 McAllister Way, Santa Cruz, CA 95060, USA
[f] Biology Department, Vancouver Island University, 900 Fifth St., Nanaimo, BC V9R 5S5, Canada

## ARTICLE INFO

## 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
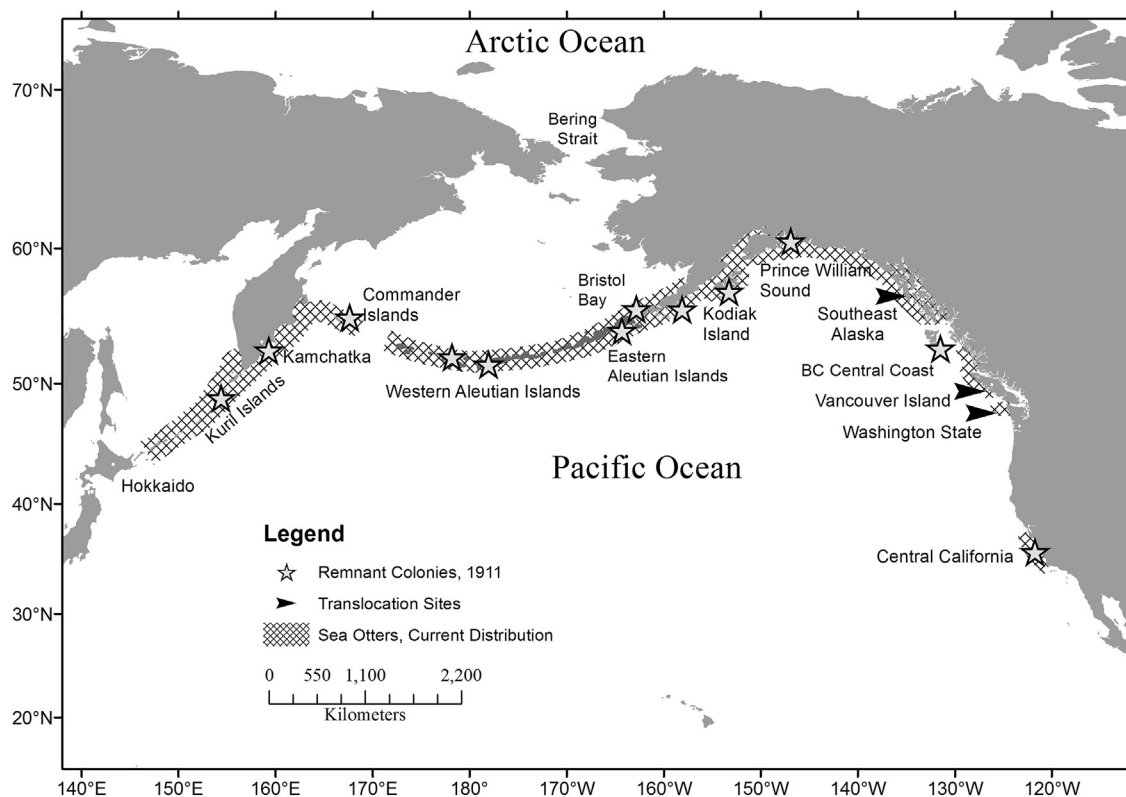
---

**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).