





The ghost of a giant – Six hypotheses for how an extinct megaherbivore structured kelp forests across the North Pacific Rim

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Abstract

Aim: The global decline of megafauna is believed to have had significant and widespread ecological impacts. One such extinction of likely important consequence is the 18th century extinction of the Steller's sea cow (*Hydrodamalis gigas*); however, little has been written about how the loss of this megaherbivore may have impacted coastal ecosystem dynamics. Drawing on historical evidence, sea cow biology, kelp forest ecology, and the ecology of extant sirenians, we propose several discrete hypotheses about the effects Steller's sea cows may have had on kelp forest dynamics of the North Pacific.

Location: North Pacific Ocean.

Time period: Pre-1760s.

Major taxa studied: Steller's sea cow (*Hydrodamalis gigas*).

Results & conclusions: The evidence we review suggests that Steller's sea cows exerted substantial direct and indirect influences on kelp forests, likely affecting the physical ecosystem structure, productivity, nutrient cycling, species interactions, and export of nutrients to surrounding ecosystems. This suggests that kelp forest dynamics and resilience were already significantly altered prior to the influence of more recent and well-known stressors, such as industrial fishing and climate change, and illustrates the important ecological roles that are lost with megafaunal extinction.

KEYWORDS

ecosystem function, extinction, herbivore, kelp forest, megafauna, Steller's sea cow, trophic cascades

1 | INTRODUCTION

No matter how well one understands kelp populations, any current program will fail to discern the ghosts of missing animals. Dayton et al. (1998)

Humanity has played a role in the decline of countless species, resulting in a rapidly accelerated extinction rate and leading many

to argue that we are currently experiencing the Earth's sixth mass extinction (Barnosky et al., 2011). One group that has been particularly susceptible to extinction are the megafauna (Ripple et al., 2015, 2019), many of which disappeared at the end of the Late Pleistocene (Barnosky, 2008; Malhi et al., 2016; Owen-Smith, 1987). Considerable effort has been devoted to understanding the drivers for the extinction of these large animals, and debate continues as to the relative contributions of climatic change and human hunting (Barnosky

et al., 2004; Broughton & Weitzel, 2018; Koch & Barnosky, 2006; P. S. Martin, 1966; Meltzer, 2020; Stewart et al., 2021). However, scientists have only recently begun to explore the ecological consequences of these extinctions (Gill, 2014; Johnson, 2009; Malhi et al., 2016; Tóth et al., 2019).

There is increasing evidence that the decline of megafauna in ecosystems around the world has markedly altered ecosystem dynamics and functions. These consequences have included nutrient cycling (Berzaghi et al., 2018; Roman & McCarthy, 2010), community composition and diversity (Faurby & Svenning, 2015; Gill et al., 2009; Janzen & Martin, 1982; Wigley et al., 2014), trophic interactions (Estes et al., 2011; Galetti et al., 2018; Janzen & Martin, 1982), climate (Smith et al., 2010), and the physical structure of ecosystems (Bakker, Gill, et al., 2016; Johnson, 2009). Much of this research has focused on the loss of apex predators and other key-stone species, such as ecosystem engineers (Estes et al., 2011; e.g., Ripple & Beschta, 2007; Roman et al., 2014); however, given their role in influencing flows of energy and system dynamics (Ehrlich & Mooney, 1983; Owen-Smith, 1987; Smith et al., 2016), the loss of any megafauna species is likely to have important ecological consequences. These consequences may be particularly pronounced when the species in question is the only representative of an entire functional group (Folke et al., 2004; Saint-Béat et al., 2015).

Marine environments have largely been spared megafaunal extinctions on the scale of terrestrial systems (Dulvy et al., 2009; McCauley et al., 2015), but centuries of human influence and declining large animal abundances mean that very few, if any, marine ecosystems can be considered unaltered by humans (Jackson, 2001; Jackson et al., 2001; Lotze et al., 2006). Even though extinctions have been rare, the consequences of reduced marine megafauna abundance are increasingly being recognized (Estes, Heithaus, et al., 2016; McCauley et al., 2015; Roman et al., 2014). In both marine and terrestrial communities we are left with simplified ecosystems and food webs where the 'ecological ghosts' of formerly influential megafauna are absent (Dayton et al., 1998).

One such marine ecosystem that has been altered by anthropogenic change, including extinctions, is kelp forests (Dayton et al., 1998; Estes et al., 1989; Jackson et al., 2001; Krumhansl et al., 2016). These highly productive ecosystems are common along rocky temperate coastlines around the world (Mann, 1973; Steneck et al., 2002), and provide numerous important ecosystem services today (Gegr et al., 2020; Smale et al., 2013) as well as throughout the Holocene (Braje et al., 2017; Corbett et al., 2008; Erlandson et al., 2007). Kelp forests of the North Pacific are also notable for being the scene of one of the only known marine megafaunal extinctions, that of the Steller's sea cow (*Hydrodamalis gigas*; Domning, 1978; Estes et al., 1989). Like many coastal ecosystems, kelp forests and their associated services are also threatened by contemporary stressors including overgrazing by echinoderms (Steneck et al., 2002), climate change (Harley et al., 2012), fishing (Steneck et al., 2013) and invasive species (Levin et al., 2002). While much has been written on these more recent changes in kelp forests (Krumhansl et al., 2016; Ling et al., 2015; Smale et al., 2013; Steneck

et al., 2002; Wernberg et al., 2019), very little is known about the role of the sea cow, and how its loss may have transformed kelp forests of the North Pacific.

Understanding the role once played by missing species, such as the sea cow, and the consequences of their extinction is essential for assessing how humans have altered kelp forest ecosystems (Dayton et al., 1998). This, in turn, is increasingly seen as central to informing the conservation and restoration of these systems (Estes, Heithaus, et al., 2016; Jackson, 2001). In this review, we ask how sea cows may have structured kelp forests of the North Pacific, and how their extinction altered ecosystem dynamics. By synthesizing historical and present ecological lines of evidence, we identify six mechanisms through which sea cows may have controlled kelp forest dynamics.

2 | STELLER'S SEA COWS AND KELP FORESTS

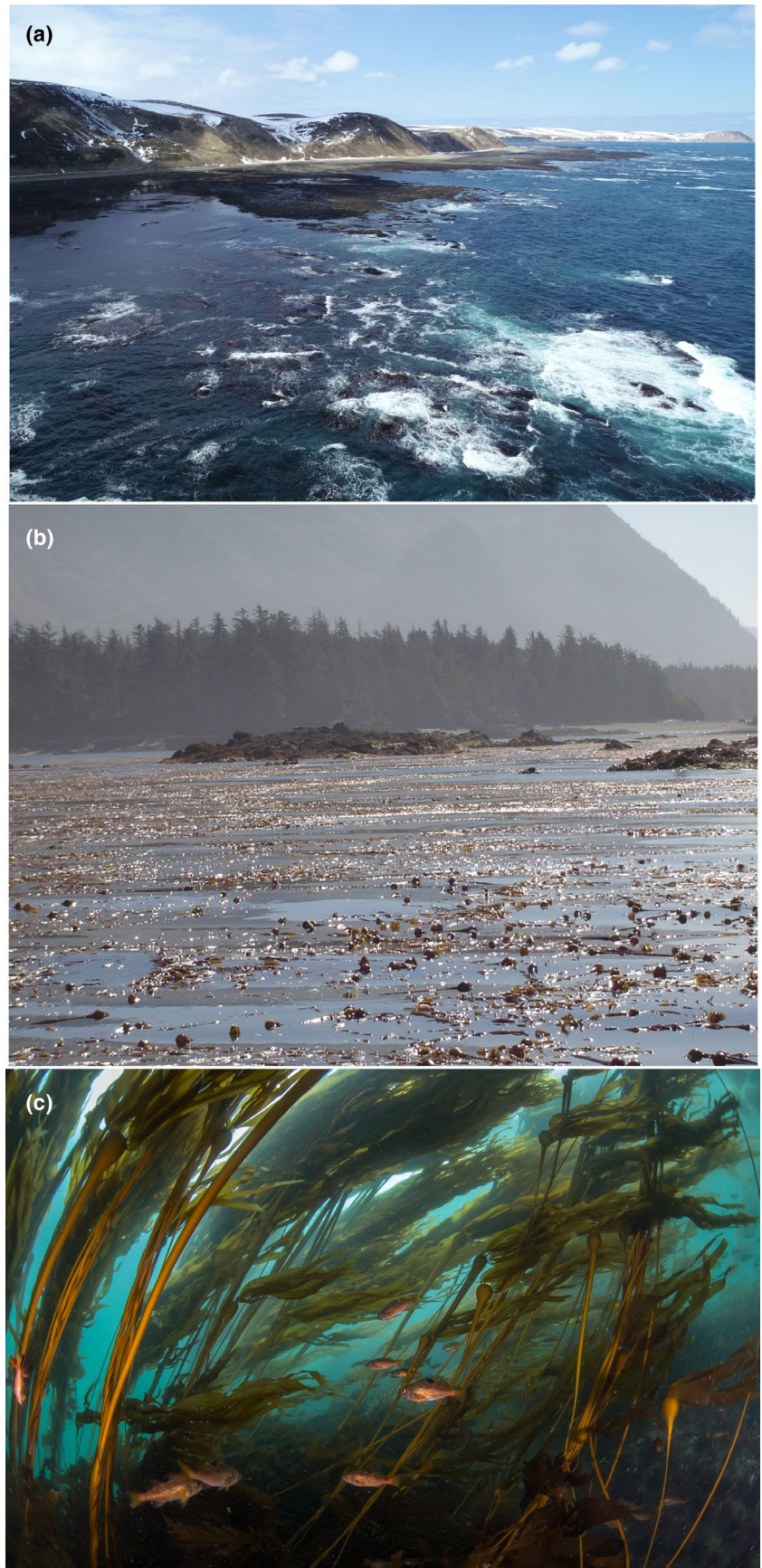
The Steller's sea cow was a large, herbivorous sirenian, first described by naturalist Georg Wilhelm Steller (Steller, 1751) while shipwrecked at the remote and uninhabited Commander Islands of the North Pacific (Figure 1a). It has been estimated that at this time the Commander Islands hosted a population of approximately 1,500 sea cows (Stejneger, 1887), but that these islands, perhaps along with other remote islands in the North Pacific (Crerar et al., 2014; Domning et al., 2007), were the final refuge of a species already in dramatic decline (Domning, 1978).

Fossil evidence suggests that at their peak, sea cows were distributed throughout the coastal waters of the North Pacific from Japan to Baja California (Domning, 1978; Domning et al., 2007). As recently as 20,000 years ago, sea cows were present along much of the North American Pacific Coast (Domning, 1978). The peopling of the Americas and subsequent Indigenous hunting is presumed to have extirpated the sea cow from much of this range (Domning, 1978; Estes, Burdin, et al., 2016; but see Sharko et al., 2021 for the suggestion that sea cow populations may have declined prior to human arrival). Though the timing of sea cow extirpation is uncertain, it is generally thought to have occurred sometime between the Late Pleistocene and the arrival of European explorers in the North Pacific, although Indigenous peoples and sea cows likely coexisted for hundreds or thousands of years (Domning et al., 2007).

The remnant population encountered and described by Steller in 1741 was subsequently lost when commercial fur hunters (primarily targeting sea otters) began visiting the Commander Islands and used sea cows as their main source of food (Stejneger, 1887). The impact of these hunting expeditions was so intense that direct overharvest of sea cows (Domning, 1978; Turvey & Risley, 2006), perhaps in combination with habitat alteration associated with loss of sea otters (Anderson, 1995; Estes, Burdin, et al., 2016), drove the sea cow to extinction by 1768 (Stejneger, 1887), less than 30 years after their description.

The sea cow was remarkable, not least because of its size, with Commander Island individuals estimated to reach more than

FIGURE 1 Images representative of habitats once occupied by the Steller's sea cow. (a) The coastline of the Commander Islands, Russia, the final location of the Steller's sea cow's extinction (photo by Evgeny Mamaev). (b) The surface of a kelp forest on the west coast of Vancouver Island, Canada (photo by Kai M. A. Chan). (c) Life below the canopy of a kelp forest near Haida Gwaii, Canada (photo by Ryan Miller)



5,000 kg in weight and 7 m in length (Domning, 1978). Based on Steller's observations, Domning (1978) further argues the Commander Islands were marginal habitat for the sea cow, and consequently the species may have been even larger elsewhere in their range where oceanographic conditions would have been more favourable (Whitmore & Gard, 1977). In addition to being so large, the sea cow appears to have been largely restricted to the surface, and is thought to have been unable to dive or submerge (Stejneger, 1887; Steller, 1751). Both observational (Steller, 1751) and morphological (Domning, 1978) evidence suggests that these giant sirenians were obligate algivores, grazers of the expansive kelp forests of the North Pacific (Estes, Burdin, et al., 2016; Stejneger, 1887; Steller, 1751). The North Pacific contains the greatest diversity of kelps on earth (Bolton, 2010; Starko et al., 2021), and sea cows almost certainly consumed a wide variety of macroalgae (Domning, 1978), including larger understory and intertidal macroalgae. However, their diet presumably consisted mainly of the dominant canopy forming kelp genera of the North Pacific, including *Nereocystis*, *Laminaria*, *Eualaria* and *Macrocystis* (depending on season and location; Dayton, 1985; Wernberg et al., 2019).

Given their aversion or inability to submerge, and rostral deflection consistent with surface feeding (Domning, 1978), sea cow grazing on kelps is likely to have been restricted to approximately the upper metre of the kelp canopy and intertidal macroalgae (Figure 1b; Anderson, 1995; Domning, 1989). It has also been noted that sea cow movement was 'sluggish' (Stejneger, 1887), with animals rarely observed far from shore, and that they preferred shallow, sheltered areas, including the mouths of rivers and creeks (Steller, 1751). This led Domning (1989) to conclude their ecological influence may have been greatest in bays, estuaries and other protected locations. Within this restricted foraging range, limited by both depth and wave exposure, sea cows are said to have grazed 'incessantly' (Steller, 1751) and were likely dependent on kelps as an abundant food source (Anderson, 1995; Estes, Burdin, et al., 2016).

Sea cow distribution across coastlines of the North Pacific would, therefore, seem to have been sensitive to the availability of their kelp forage, as well as other environmental conditions. Specifically, seasonality in macroalgae availability (particularly annual species of kelp such as *Nereocystis* and *Eualaria*) likely limited sea cow populations and distributions. This rationale is supported by Steller's observation of winter emaciation and starvation amongst sea cows at the Commander Islands (Steller, 1751). Other life-history requirements may have also restricted sea cow distribution. For example, it is not known whether Steller's sea cows were dependent on sources of fresh water (like the West Indian manatee, Ortiz et al., 1998) or obtained water from other means (i.e., through diet or sea water as appears to be the case for dugongs, Smoll et al., 2020). A requirement for fresh water would have substantially restricted available habitat. Similarly, calving may have required sheltered areas protected from wave exposure or other threats (as is the case with some other marine mammals, e.g., Rayment et al., 2015), which would have also limited their distributions.

Despite their likely heterogeneous distribution, sea cows would nevertheless have been an important source of herbivory where they did occur. As with other marine megafauna with a large influence on marine ecosystems (Christianen et al., 2019; Estes, Heithaus, et al., 2016), the sea cow's large body size and appetite would likely have translated into a considerable impact on kelp forests (Estes et al., 1989; Pitcher, 1998). Thus, to better understand how kelp forests have been altered by humans, one must consider the ecological role of this extinct megaherbivore.

3 | LINES OF EVIDENCE

In the absence of ecological research from the pre-extinction period, we rely on other sources of knowledge to consider how Steller's sea cows might have interacted with and altered the ecosystem in which they lived. These include historic descriptions of live animals, the fossil record, and extrapolation from present analogues. Here, we review and synthesize knowledge from all three approaches to explore the role once played by Steller's sea cows.

Historic data from ships' logs, naturalists' notes, and oral histories provide some insight into sea cow ecology. Steller's detailed notes on sea cow behaviour and his description of a dissection of an adult female sea cow (Steller, 1751) are an invaluable and rare source of knowledge for this extinct megafauna. Corroborating evidence can also be found in the human histories and archaeological records of the Aleutian Islands (Corbett et al., 2008; Domning et al., 2007). However, the interpretation of these historical records is not always straightforward (Pooley, 2018), and requires a recognition of limitations and context (Taylor, 2013). For instance, 'sea cows' have been mentioned since their apparent extinction in the late 18th century in the journals and ships' logs of several explorers and sailors, notably L. M Turner at Attu Island (cited in Domning et al., 2007). There have also been reports of sea cows south-east of the Aleutian Islands on the coast of what is now western Canada (Jewitt, 1807; Meares, 1790), but these records have not been substantiated with archival or archaeological research (McKechnie & Wigen, 2011).

Additional insight into the biology of extinct species may be gained through the study of fossil remains. This approach is increasingly seen as a valuable source of knowledge for many globally extinct species and degraded ecosystems (Dietl & Flessa, 2011; Rick & Lockwood, 2013). In the case of sea cows, Domning (1978) conducted an extensive review of sirenian evolution in the North Pacific, paying special attention to the distribution and biology of Steller's sea cow (also see Anderson, 1995; Crerar et al., 2014; Domning et al., 2007; Stejneger, 1887). The understanding of sea cow evolution, physiology, and life history gained from this past work is robust and, while not restated herein, serves as the basis for further discussion of sea cow ecology and functional role.

However, our understanding of sea cows from direct study is limited in scope, and largely unable to shed light on ecological dynamics. To examine ecosystem processes and species interactions lost through species extinctions, we examine present-day ecosystem

dynamics and the role of extant, potentially analogous species. Fortunately, North Pacific kelp forest dynamics – particularly in relation to herbivory – have received extensive attention and provide a robust framework within which to examine the role of sea cows (e.g., Dayton, 1985; Steneck et al., 2002). Systems where large grazers still exist or have been lost more recently, as well as ecological theories derived from the study of such systems (e.g., McNaughton, 1985; Owen-Smith, 1987), serve as analogous systems, and can thus also provide insights into the consequences of lost sea cow grazing in kelp forests. The closest extant species to the sea cow is the dugong (*Dugong dugon*), an important grazer in tropical seagrass ecosystems (Preen, 1995; Valentine & Duffy, 2006) that is currently critically endangered through much of its range and a useful analogue for understanding Steller's sea cows.

4 | HYPOTHESIZED EFFECTS ON COMMUNITY STRUCTURE AND ECOSYSTEM FUNCTION

Large herbivores play important roles in many ecosystems (Bakker, Pagès, et al., 2016; McNaughton et al., 1997; Ripple et al., 2015), and their loss has significant effects on ecosystem processes (Doughty, 2017; Gill, 2014; Johnson, 2009; Ripple et al., 2015). The sea cow is likely to have been similar, especially as sirenians co-evolved with North Pacific kelp forests for at least 8–10 million years (Domning, 1978, 1989; Estes & Steinberg, 1988). Given their large size and 'incessant' grazing (Anderson, 2002; Steller, 1751) it is likely sea cows would have been a notable source of herbivory for shallow and canopy kelps (Domning, 1989). The intensity of this herbivory and its subsequent effects would almost certainly have been density dependent, and varied geographically in response to sea cow distribution and habitat preferences (Domning, 1989; Lubchenco & Gaines, 1981; Scott et al., 2021).

The effects of sea cow herbivory on kelp canopies in the North Pacific would also have differed substantially from extant herbivores, such as sea urchins, which often graze on kelp holdfasts (Filbee-Dexter & Scheibling, 2014; Mann, 1988; Stevenson et al., 2016), thereby causing the loss of entire kelps. In contrast, sea cow grazing would have only consumed kelp close to the surface (Figure 1b), leaving much kelp biomass attached and intact. Such herbivory would have had very different ecological impacts from today's more disruptive and less consumptive grazing by sea urchins. Consideration of the available lines of evidence led us to develop six hypothesized impacts of sea cow herbivory in kelp forests (Table 1 and Figure 2). We discuss each of these in turn.

4.1 | Physical ecosystem structure

Sea cows grazing upon canopy kelp likely modified the abundance and composition of kelp and kelp-associated species. Given their intense grazing (Steller, 1751), sea cows likely reduced canopy and

littoral kelp biomass substantially in shallower waters (Table 1). In subtidal areas where sea cows would have grazed primarily at the surface, a reduced kelp canopy may have allowed an increase in understory macroalgae biomass due to increased light availability (see following section; Estes et al., 1989; Miller et al., 2011; Reed & Foster, 1984). The influence of canopy reduction on understory macroalgae is likely to have varied geographically, along with differences in macroalgae species and competitive interactions (Dayton, 1975; Edwards & Connell, 2012). For instance, while canopy forming kelps are competitively dominant in much of the North Pacific (Edwards & Connell, 2012; Reed & Foster, 1984), in the Aleutian Islands the canopy forming kelp *Eualaria* seems to be subordinate to the understory (Dayton, 1975).

Both canopy and understory kelps are known to play important structural roles in rocky reef ecosystems (Figure 1c), providing complex three-dimensional habitat for numerous species (Duggins, 1988; Markel, 2011; Markel & Shurin, 2015; Teagle et al., 2017), altering hydrodynamic flow (Eckman et al., 1989), and increasing larval retention and survival (Duggins et al., 1990; Eckman & Duggins, 1991). Given the documented ecosystem effects of kelp biomass reduction by other herbivores, predominately sea urchins (Dayton, 1985; Filbee-Dexter & Scheibling, 2014; Ling et al., 2015; Wilmers et al., 2012), it is likely that sea cow grazing would have also altered the physical structure of the ecosystem and many of these important processes (Figure 2). It has additionally been suggested that by increasing abundance of understory macroalgae, sea cows may have decreased the abundance of benthic suspension feeders (e.g., bivalves, tunicates, bryozoans, etc.) that compete for space with understory macroalgae (Arkema et al., 2009; Estes et al., 1989).

Sea cow herbivory would therefore seem to constitute a top-down influence on kelp biomass and habitat structure now absent from North Pacific kelp forests. The spatial limits of sea cow grazing (i.e., only shallow and surface kelp) differ markedly from other herbivores such as sea urchins (Estes et al., 1989), and it is unlikely sea cows could have locally extirpated kelp forests as sea urchins do, especially given the difference in grazing behaviour. Thus, while sea cows undoubtedly consumed a considerable amount of kelp, the magnitude of their impact on kelp biomass and the consequences for ecosystem functions such as habitat structure and larval retention remain uncertain. However, any such impacts were likely quite different from those of benthic grazers. Whatever influence they would have had was likely spatially and geographically heterogeneous, and would have worked in concert with other forms of disturbance, such as invertebrate herbivory and wave stress.

4.2 | Primary productivity

Sea cow grazing may have boosted kelp forest productivity through compensatory growth and increased light availability. Kelp forests are one of the most productive ecosystems in the world (Mann, 1973), providing much of the production in many temperate coastal systems (Krumhansl & Scheibling, 2012;

TABLE 1 Summary of hypothesized effects of Steller's sea cow herbivory on the structure and dynamics of kelp forests of the North Pacific

Ecosystem effects	Description	Potential consequences
1 Physical ecosystem structure	Sea cow herbivory of intertidal and canopy kelp likely altered the physical structure and community dynamics of kelp forests. Spatially restricted sea cow grazing would have decreased littoral and surface macroalgae biomass, influencing competition amongst macroalgae and likely increasing understory macroalgae biomass and diversity in some regions.	Decreased macroalgae biomass near the surface Increased understory kelp biomass and diversity Altered biogenic habitat complexity, hydrodynamic flows, and patterns of larval settlement
2 Primary productivity	Through the consumption of kelp fronds, sea cow herbivory may have encouraged compensatory growth in grazed canopy kelps, and reduced light limitation resulting in increased productivity in understory kelp and phytoplankton.	Compensatory growth in grazed kelps Increased productivity of phytoplankton and understory seaweeds Maintained (or increased) overall system productivity
3 Nutrient cycling and availability	Through physical disturbance during grazing as well as the digestion of kelp biomass sea cows may have accelerated nutrient cycling and increased food and nutrient availability.	Increased cycling and availability of kelp-derived nutrients and detritus Increased secondary productivity throughout ecosystem, particularly in suspension feeders
4 Mediation of predator–prey interactions	Sea cows may have increased the availability of drift kelp and associated nutrients (hypothesis 3) and abundance of understory macroalgae (hypothesis 1), altering the vulnerability of prey and mediating predator–prey interactions such as the vulnerability of large mobile invertebrates to sea otter predation.	Reduced prey foraging times and vulnerabilities Increased invertebrate biomass and diversity due to expanded refuge from sea otter predation
5 Kelp export	Grazing by sea cows, and an increase in kelp detritus (hypothesis 3), may have altered the amount of kelp exported from kelp forests. The year-round disturbance by sea cows (as opposed to seasonal wave stress) may also have resulted in less seasonality in this export.	Altered magnitude and seasonality of kelp export Changes in secondary productivity of receiving habitats
6 Biotic dispersal	Sea cows may have enhanced kelp recruitment and dispersal through physical grazing and/or the ingestion and transportation of spores. Kelp spores associated with sea cow faeces may have experienced altered survival rates.	Increased spore dispersal distance Changes in spore dispersal dynamics Facilitated colonization of new areas and kelp genetic exchange

Steneck et al., 2002). While grazing by sea cows would have reduced standing kelp biomass, it does not necessarily follow that primary productivity would be similarly reduced (Table 1). Both compensatory growth and increased light availability could compensate for the effect of sea cow herbivory on kelp biomass.

Compensatory plant growth as a response to herbivory is described in a variety of terrestrial (reviewed in McNaughton, 1983; Stowe et al., 2000) and marine systems such as seagrasses (Valentine & Duffy, 2006) and some kelps (Cerde et al., 2009; Franco et al., 2017; Gao et al., 2013). Most notably, *Macrocystis* (a dominant kelp of the Northeast Pacific) has been found to exhibit a large capacity for regrowth in response to commercial harvest (Krumhansl et al., 2017) [but see Geange (2014) for a counter example], a process that removes only the floating canopy in a manner likely similar to how sea cows may have grazed on canopy kelps. Krumhansl et al. (2017) found that individual *Macrocystis*

canopies recovered from harvest at a rate of 4–30 cm/day, resulting in the recovery of 35–150% of pre-harvest canopy biomass after 4 weeks. This suggests that grazing by sea cows on *Macrocystis*, and perhaps other kelps of the North Pacific, may have encouraged rapid regrowth at a similar pace in grazed kelps. Similar processes, termed cultivation grazing, have been described for modern dugong and manatee grazing on seagrass (Lefebvre et al., 1999; Preen, 1995). Sea cow consumption of canopy biomass may have also reduced the wave stress experienced by kelps, causing less canopy kelp to be detached during winter storms. This would have left more photosynthetic biomass remaining through the winter, potentially increasing growth rates and productivity in the spring. However, other kelps of the North Pacific with different life histories and meristem locations (e.g., *Nereocystis*) may have a lower capacity for regrowth, and thus be more impacted by canopy removal (Roland, 1985; Springer et al., 2007). As in

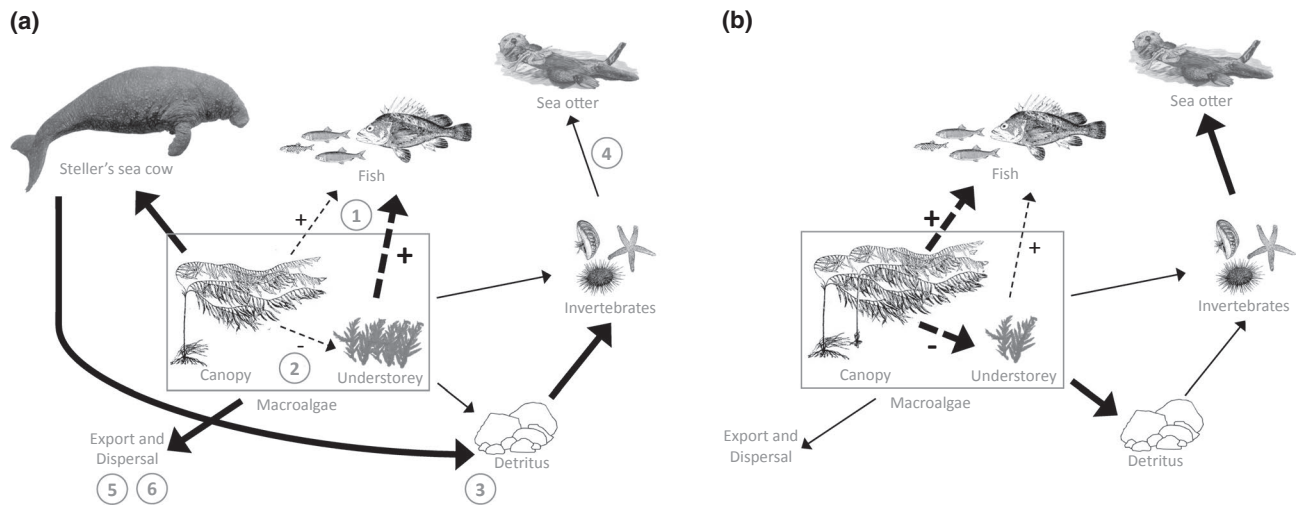


FIGURE 2 Kelp forest interaction web in the presence and absence of Steller's sea cows. Simplified interaction web illustrating material flows (e.g., trophic flows, solid arrows) and indirect interactions (dashed arrows, positive or negative effects shown with '+' and '-') in the presence (a) and absence (b) of Steller's sea cows. The weight of the line corresponds to the relative strength of the interaction in the two system states. Numbers in (a) correspond to the six hypothesized effects of Steller's sea cow herbivory: 1 = physical ecosystem structure; 2 = primary productivity; 3 = nutrient cycling and availability; 4 = predator-prey interactions; 5 = kelp export; and 6 = biotic dispersal. See the list of reproduced images for image citations

other grazing systems (Dyer, 1982; McNaughton, 1983), the importance of compensatory growth in sea cow forage was likely density and condition dependent, and would have varied with grazing intensity and environmental conditions (e.g., Oshurkov & Ivanjushina, 1993).

Sea cow grazing may also have increased light availability, an important driver of kelp forest productivity and composition, as algae and phytoplankton compete for light as well as other nutrients (Dayton et al., 1984; Desmond et al., 2015; Steneck et al., 2002). Canopy-forming kelps in particular can reduce light availability on rocky reefs (Reed & Foster, 1984). This shading has been shown to limit productivity and recruitment of other algal species (Borchers & Field, 2009; Reed & Foster, 1984). In many regions of the North Pacific, removal of canopy kelps results in significant increases in productivity of phytoplankton and understorey macroalgae (Miller et al., 2011), as well as juvenile macroalgae recruitment (Edwards, 1998; Reed & Foster, 1984; Santelices & Ojeda, 1984). Miller et al. (2011) found that the increased productivity from understorey algae can completely compensate for lost canopy kelps, resulting in total productivity remaining relatively constant.

In sum, while sea cow herbivory would have reduced kelp biomass, increased productivity and compensatory growth in response to grazing, in combination with increased light availability, likely counteracted any kelp biomass reduction and may have maintained or even increased the overall productivity of the system (Figure 2). Given the importance of macroalgal productivity to coastal ecosystems (Duggins et al., 1989; Steneck et al., 2002), an increase in productivity caused by sea cows would have had substantial implications for nutrient availability throughout coastal ecosystems.

4.3 | Nutrient cycling and availability

Large herbivores play a critical role in accelerating nutrient cycling in a variety of terrestrial ecosystems, accelerating turnover and liberating nutrients stored in standing plant biomass (Hobbs, 1996; Malhi et al., 2016; Tanentzap et al., 2013; Zimov et al., 1995). Megafauna may also influence the availability of food and detritus for other organisms in the ecosystem (Estes, Heithaus, et al., 2016; Galetti et al., 2018; Schmitz et al., 2010; Terborgh & Estes, 2013). Large herbivores likely play similar roles in marine systems. For example, sea turtles and sirenians have been shown to alter nutrient availability, accelerate decomposition, and provide nutrient rich food for detritivores in seagrass ecosystems (Domning, 2001; Thayer et al., 1982, 1984). Sea cows would have also contributed to the cycling and availability of food and nutrients through both the digestion of kelp biomass and the physical grazing process (Table 1).

The digestive process of sea cows, like other large herbivores, would have accelerated decomposition, nutrient cycling, and detrital production in kelp forests. Available evidence suggests that the sea cow used hindgut fermentation to assist in the digestion of its kelp forage. The evidence includes the presence of hindgut fermentation in sirenians globally (Best, 1981; Murray et al., 1977; Thayer et al., 1984), and Steller's observation that the sea cows' digestive tract, and the faeces itself, were similar to those of a horse (Steller, 1751). It is therefore probable that sea cows returned nutrient-rich kelp biomass to the system through faecal production. These nutrient-rich faeces would have been an important source of nutrients for detritivores and suspension feeders (Figure 2), many of which are influenced by organic detritus (Duggins et al., 1989). The important role of marine mammal

waste in nutrient cycles has previously been recognized in other contexts; for example, whale faeces have been shown to be an important source of iron acting as a fertilizer in much of the world's oceans (Doughty et al., 2015; Nicol et al., 2010; Roman & McCarthy, 2010). However, the importance of sea cow-mediated nutrient recycling for primary productivity may have been limited, given the generally nutrient-rich nature of North Pacific seawater (J. H. Martin & Fitzwater, 1988; Moore et al., 2013).

The sea cow would have also increased the bioavailability of particulate organic matter simply through mastication. The grazing of the toothless sea cows (Domning, 1978; Steller, 1751) seems likely to have left a trail of kelp fragments in their wake. Indeed, Steller observed that where sea cows grazed, large amounts of discarded kelp were seen washed up on the shore (Steller, 1751). Much like drift kelp and kelp detritus in present-day kelp forests (Duggins et al., 1989; Feehan et al., 2018), this discarded kelp would have been an important source of primary production to numerous coastal species. In addition, discarded kelp washed up on the shore, as Steller observed (Steller, 1751), may have been an important source of nutrients to terrestrial ecosystems (Dugan et al., 2011; Polis & Hurd, 1996). Therefore, by accelerating nutrient cycling and increasing the availability of particulate organic matter, sea cows would likely have magnified secondary productivity (Dugan et al., 2011; Duggins et al., 1989).

The significance of sea cows to nutrient cycling is particularly notable given the lack of herbivory in many kelp forest systems today (Duggins, 1988). In present-day kelp forests, the majority of kelp biomass is not directly consumed, but enters the food web indirectly, as particulate or dissolved organic matter (Duggins et al., 1989; Gerard, 1976; Harrold & Pearse, 1987). Krumhansl and Scheibling (2012) estimated that as much as 82% of global kelp productivity enters the detrital pathway. In the presence of sea cows, a much larger percentage of kelp biomass would have entered the food web as particulates, faeces, or sea cow biomass, representing potentially important changes in the flow of kelp-derived production. Similar arguments for the historic importance of herbivory have been made in other ecosystems, most notably for seagrass meadows (Domning, 2001; Valentine & Duffy, 2006). Domning (2001) argued that

the long-established tenet that seagrass ecosystems are largely detritus-based... must be revised to recognize that the modern situation is anomalous, and that the "normal" pattern throughout most of tropical seagrass history has been that much (probably most) of the primary productivity has been channeled through the guts of herbivores, particularly sirenians.

In the same fashion, today's understanding of kelp forests as largely detritus- and particulate-based (e.g., Duggins et al., 1989) may be a relatively recent development caused in part by the extinction of the sea cow.

4.4 | Mediation of predator–prey interactions

The effects of sea cow herbivory hypothesized above may have mediated predator–prey interactions, including those involving sea otters, a keystone predator of kelp forests. Mediating relationships – the indirect effect of a third species on the trophic relationship between two species – are a common and important aspect of marine communities (Dill et al., 2003; Werner & Peacor, 2003), including kelp forests (Espinosa-Romero et al., 2011; Lee et al., 2016; Markel & Shurin, 2015). The changes to ecosystem dynamics discussed above suggest that the presence of sea cows may have indirectly affected kelp forest communities by mediating interactions between other species. The tightly linked trophic relationship between kelp, sea urchins, and urchin predators such as sea otters has been well studied (e.g., Estes & Palmisano, 1974; Gregor et al., 2020; Watson & Estes, 2011), and is one relationship that sea cows may have mediated (Table 1).

The mechanism for mediating the kelp–sea urchin–sea otter relationship rests on the increased kelp bioavailability described above. When sea urchins or other mobile invertebrates receive an adequate supply of drift algae and detritus, they do not emerge from crevices and other refugia to forage on kelp (Dayton et al., 1998; Krumhansl & Scheibling, 2012; Lee et al., 2016). Similarly, urchins located in relative safety below the foraging depth limit of sea otters may not enter shallow waters if they receive adequate forage. By increasing the availability of drift kelp, sea cows would have increased food supplied to sea urchins in these protected habitats, allowing them to remain sheltered from sea otter predation. This mediating effect would have substantially altered the trophic dynamics of this keystone predator and coastal ecosystems generally (Figure 2; Gregor et al., 2020).

4.5 | Kelp export

Sea cow herbivory, according to the processes described above, would have also changed the amount and nature of the primary production exported from kelp forests to adjacent ecosystems (Figure 2), where such nutrients can be a limiting resource (Polis & Hurd, 1996; Vetter, 1995). Export of kelp biomass to shorelines, subtidal habitats, and the deep sea can represent significant nutrient subsidies and spatial linkages between these ecosystems (Gregor et al., 2020; Harrold et al., 1998; Steneck et al., 2002) and was reported by Steller (1751). Kelp export today is primarily driven by wave action and currents (Cavanaugh et al., 2011; Filbee-Dexter & Scheibling, 2012; Krumhansl & Scheibling, 2012; Saunders, 2014), but other factors such as temperature, encrusting invertebrates, herbivory, and trophic dynamics also contribute to detrital production and export (Duggins et al., 2001; Gregor et al., 2020; Krumhansl & Scheibling, 2011, 2012). In addition to contributing nutrient subsidies to surrounding habitats, dislodged kelp can create drifting seaweed rafts with diverse associated communities (Rothäusler et al., 2012; Saunders, 2014). Thinning of kelp canopies by sea cows

would have also reduced the drag experienced by kelps, potentially reducing their risk of detachment due to wave stress. The combined effects of sea cows on kelp export were thus likely substantial and far-reaching, but also density-dependent, and a function of oceanographic and bathymetric heterogeneity (e.g., Wickham et al., 2020).

Sea cow herbivory may also have affected the timing of kelp export. Today's kelp export is strongly influenced by seasonal storms and currents (Saunders, 2014; Sousa, 1985; Tegner et al., 1997). The year-round grazing of sea cows may have altered this seasonal cycle (Estes et al., 1989), providing a more constant flow of kelp to surrounding habitats. The consequence of such a change in timing is largely unpredictable, but would likely influence the life history of detritivores. For instance, growth rates of the mussel *Mytilus californianus* are strongly influenced by both food abundance and temperature (Menge et al., 2008). This species might therefore be expected to benefit from greater availability of kelp-derived nutrients in warmer months. By encouraging a more reliable export of kelp biomass, sea cow herbivory likely supported increased consumer growth and abundance in adjacent habitats.

4.6 | Biotic dispersal

By consuming kelp, sea cows may have facilitated kelp recruitment and dispersal – either directly or via compensatory plant responses. Terrestrial plants are known to use animals as vectors for seed dispersal, although little is known about biotic dispersal of marine angiosperms such as seagrasses (Tol et al., 2017), and even less about seaweeds. Spores of marine algae have been found on the legs of amphipods and, together with vegetative fragments, have been reported to survive digestion by fish and molluscs (Buschmann & Bravo, 1990; Santelices & Paya, 1989) but not echinoderms (Skern et al., 2003). And while the role of extant sirenians (i.e., manatees and dugongs) in seagrass seed dispersal has been widely discussed (Marsh et al., 2011; McMahon et al., 2014) only recently has it been demonstrated that biotic dispersal of tropical seagrass seeds (by dugongs and green sea turtles) enhances connectivity amongst seagrass meadows across large spatial extents (Tol et al., 2017).

Dispersal of kelp spores has long been thought to depend primarily on oceanographic factors, like currents, waves and tides (Bernardes Batista et al., 2018; Gaylord et al., 2004, 2006; Norton, 1992), although the processes are still not well understood (Dobkowski et al., 2019; Gaylord et al., 2006). Dispersal by these mechanisms is highly variable, largely restricted to within a few metres of adults although dispersal of several kilometres is possible (Gaylord et al., 2002; Reed et al., 1988). Additionally, long-lived microscopic life stages of kelps are thought to play important roles in the persistence and recruitment of kelp populations under variable environmental conditions (Edwards, 1998, 2000). It seems intuitive that kelp species would have developed co-evolutionary relationships with sea cows to allow for long-term co-existence, especially regarding their reproductive tissues. Such adaptations could take

the form of chemical deterrents (Estes & Steinberg, 1988); excess production of spores to compensate for grazing; allocation of reproductive tissues nearer the bottom (as in *Eualaria fistulosa*; Estes et al., 1989); or developing mutualistic strategies to benefit from grazing, such as 'seed' dispersal.

Nereocystis would be especially sensitive to canopy grazing, due to the location of spore-producing sori at the margins of the fronds (Druehl & Clarkston, 2016; Roland, 1985). The physical grazing of sea cows was therefore likely to have detached sori, potentially facilitating the dispersal of *Nereocystis* spores. Furthermore, the ingestion of reproductive tissue by sea cows may have led to the dispersal of macroalgae spores in sea cow faeces. Although the zoospores of brown algae lack a cell wall and seem to be sensitive to high temperatures (Hoffmann & Santelices, 1991; Lind & Konar, 2017), it has been reported that the gametophytes of some kelp species may remain dormant for months, withstanding environmental factors inadequate for normal development and survival (Dobkowski et al., 2019; Edwards, 2000). Thus, while spore tolerance to digestion remains uncertain (Cabral de Oliveira, 1991; Lind & Konar, 2017; Skern et al., 2003), the spores of some kelp species may have been able to withstand digestion by sea cows and be dispersed in their faeces. As with biotic dispersal in other systems (e.g., Kendrick et al., 2012), these potential mechanisms would have promoted recruitment and colonization of new areas and facilitated genetic exchange (Reed, 1990; Reed et al., 1988).

4.7 | Other processes

Like other large herbivores (Galetti et al., 2018; Ripple et al., 2014, 2015), sea cows would have also served as prey for a variety of species. Steller observed that while foraging, sea cows with calves were careful to keep their calf between themselves and the shore (Steller, 1751), suggesting vigilance of predation from the open ocean. The most likely source of this predator avoidance behaviour would seem to be transient killer whales (*Orcinus orca*) and sharks (Domning, 1978). Transient killer whales in particular are known to prey upon a variety of marine mammals (Jefferson et al., 1991), and while we have no direct evidence for killer whale predation on sea cows, their ability to prey upon both large baleen whales and other sirenians such as dugongs (Jefferson et al., 1991), and the adaptation of local killer whale populations to endemic prey (Lopez & Lopez, 1985), strongly suggest that sea cows experienced killer whale predation.

Not least amongst the predators of sea cows were humans. Buoyant, stationary, and dependent on coastal macroalgae, sea cows would have been easily accessible to hunters, providing an important food source for early Indigenous peoples of the North Pacific (Domning, 1978; Stejneger, 1887). Human predation on sea cows is thought to have been so intense – and sea cows so vulnerable (Stejneger, 1887) – that it contributed to their extirpation from inhabited areas of the North Pacific Rim (Domning, 1978; Turvey & Risley, 2006), and their final extinction at the Commander Islands (Domning, 1978; Pitcher, 1998).

Finally, Steller often observed birds perching on the exposed backs of sea cows, apparently feeding on a marine parasite that infested their skin (Domning, 1978; Steller, 1751), much like the oxpecker (Buphagidae) on large mammals of southern Africa (Galetti et al., 2018; Plantan et al., 2013). Diverse linkages between kelp forests and bird communities have been previously described (e.g., Anthony et al., 2008; Irons et al. 1986; Rechsteiner et al., 2018); however, the mutualistic (or perhaps parasitic) relationship between seabirds and sea cows is another intriguing relationship that would have disappeared along with the sea cow.

5 | DISCUSSION

The extinction of megafauna that once populated marine and terrestrial ecosystems is increasingly understood to have had important and widespread ecological implications, yet these extinct species are often overlooked in the study of present-day ecosystems. This review suggests that the consequences of defaunation were often multiple and profound, and considering these missing species may provide valuable insights into current ecological dynamics. In the case of the Steller's sea cow, the evidence reviewed here suggests they played an important role in North Pacific kelp forests, and that the historical ecosystem dominated by this megaherbivore would have been very different from the kelp forests of today. The six ecological hypotheses examined here outline several ways sea cows may have helped structure ecosystems of the North Pacific, and illustrate how much human-driven extinctions may have altered ecosystems over historical time-scales.

The diverse lines of evidence reviewed above indicate that sea cows played an important role in controlling the structure and flow of energy within the system, and that their extinction substantially constrained ecosystem function (Ehrlich & Mooney, 1983). Although herbivores, sea cows likely exerted a strong top-down influence on kelp forests. Based on the evidence presented herein, it is reasonable to conclude that a sea cow-dominated system would have had a fundamentally different structure, with important consequences for species diversity and abundance, primary and secondary productivity, and the flow of energy and biomass amongst trophic levels and habitats.

Furthermore, the extinction of the sea cow constituted the loss of an entire functional group that influenced ecosystem dynamics across numerous scales with significant implications for resilience (Folke et al., 2004; Peterson et al., 1998). Specifically, the loss of the numerous direct and indirect interactions would have reduced ecosystem resilience (Saint-Béat et al., 2015; Smith et al., 2016). This understanding of sea cows as controllers of kelp forest structure and energy flows is consistent with our understanding of the role of many other terrestrial megafauna (Enquist et al., 2020; Galetti et al., 2018). As we have argued for sea cows, research on other extinct or drastically reduced megafauna has highlighted their important influence on ecosystem structure (Bakker, Gill, et al., 2016; Johnson, 2009), biogeochemical cycles

(Doughty et al., 2015; Roman & McCarthy, 2010), and trophic interactions (Estes et al., 2011). In many cases the historical decline of megafauna and associated decreases in resilience occurring centuries or millennia ago may have set the stage for more recent and ongoing ecological collapse (Estes et al., 2011; Jackson et al., 2001; Owen-Smith, 1987). Considering the influence of missing species in ecosystems around the globe, as we have begun to do here for kelp forests, may broaden our understanding of both past and present ecological dynamics. Failing to consider the important roles played by these extinct species would be to neglect the history that has shaped the present system and succumb to the syndrome of shifting baselines (Dayton et al., 1998; Pauly, 1995; Soga & Gaston, 2018).

The evidence reviewed above provides support for all six hypotheses, and suggests multiple likely consequences (Table 1). Several of these hypotheses (e.g., changes in ecosystem structure and primary productivity) can draw upon known kelp forest dynamics, allowing greater insight into the consequences of sea cow extinction. Others, however, have limited direct analogues and require extrapolating from other systems (e.g., biotic dispersal), or may build upon kelp forest dynamics that are less well understood (e.g., kelp export). In such cases, the implications of these processes for ecosystem dynamics may be less clear. This necessarily speculative approach means we cannot predict the relative influence of the processes discussed here or the magnitude of their effects. Nonetheless, the available evidence suggests that all six hypotheses would have had important consequences for the ecological dynamics of kelp forests, and the wider North Pacific.

Understanding changes in coastal ecosystem dynamics resulting from the extinction of the sea cow is particularly important given the role of kelp forests in supporting economically and culturally valuable species. Kelp forests contribute to a variety of ecosystem services such as food provisioning (Markel, 2011) and carbon sequestration (Wilmers et al., 2012) amongst several others (Filbee-Dexter & Wernberg, 2018; GREGG et al., 2020; Martone et al., 2020; Smale et al., 2013). The diminished ecosystem function in the absence of sea cows has almost certainly reduced the production of these ecosystem services. For instance, the changes in primary productivity, kelp export, and spore dispersal would have reduced both the export and sequestration of primary production, while sea cow-mediated predator-prey dynamics and nutrient availability (as particulate organic matter) would have altered the abundance of important fish and invertebrate species. Thus, the changes ascribed to more recent and well-described impacts such as hunting of marine mammals for pelts (Estes et al., 1989; Kenyon, 1969), industrial fishing (Jackson et al., 2001; Steneck et al., 2013), and climate change (Arafteh-Dalmau et al., 2019; Harley et al., 2012) further modified an already impacted system that was already quite different from its historical, more resilient state.

The sea cow is one of many examples where a valuable species has been lost, and the restoration of trophic interactions and ecosystem functions could help maintain and improve desired ecosystem states (Corlett, 2016; Donlan et al., 2006; Lundgren et al., 2018; Svenning et al., 2016). Approaches to functional restoration have included

rewilding and species substitutions (Griffiths et al., 2013; Guyton et al., 2020; Zimov et al., 1995), often – but not always – with positive results (Ehrlich & Mooney, 1983; Seddon, Griffiths et al., 2014). In the case of the globally extinct sea cow, no analogous taxa exist in the North Pacific, so restoration would depend on active ecosystem management, or possibly the emerging and controversial concept of de-extinction (McCauley et al., 2017; Seddon, Moehrensclager, et al., 2014). Given the scale and significance of the potential sea cow effects we have explored here, any restoration of sea cow influence to the North Pacific would likely have a substantial impact on ecosystem dynamics, resilience, and the provision of ecosystem services. Similarly, restoration and conservation efforts in other ecosystems would be remiss to neglect the roles once played by extinct or extirpated species.

6 | CONCLUSION

We live on a planet denuded of its megafauna. Where large animals were once more numerous, we are left at best with diminished populations, or at worst with only the archaeological and ecological legacies of their existence. Careful examination of these ecological ghosts can shed light on what ecosystems may have looked like in their presence, and how millennia of human influence have shaped life on our planet. Understanding these historical changes – not just over decades or centuries, but millennia – is vital for effective conservation and restoration of ecosystems and their associated ecosystem services.

By drawing on sea cow biology, kelp forest ecology, and analogous herbivores, our review provides insight into the important role of Steller's sea cows in kelp forests, and the broader North Pacific Ocean. While it is challenging to predict the complex effects sea cows may have had in kelp forests, it is even harder to imagine these large grazers having no effect on their surrounding ecosystem. Considering the disproportionate role megafauna once had globally (Enquist et al., 2020), understanding these interactions is essential for the accurate description of historic ecological baselines and informing future restoration efforts.

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CONFLICT OF INTEREST

The authors declare no competing interests.

AUTHOR CONTRIBUTIONS

KC and EG conceived of the research; CB and KC designed the research, CB, AC and KC conducted the research; CB and AC wrote the manuscript with significant contributions from all authors; and EG, IM and KC supervised the research.

DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analysed in this study.

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BIOSKETCH

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