

Sea otters, kelp forests, and the extinction of Steller's sea cow

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The late Pleistocene extinction of so many large-bodied vertebrates has been variously attributed to two general causes: rapid climate change and the effects of humans as they spread from the Old World to previously uninhabited continents and islands. Many large-bodied vertebrates, especially large apex predators, maintain their associated ecosystems through top-down forcing processes, especially trophic cascades, and megaherbivores also exert an array of strong indirect effects on their communities. Thus, a third possibility for at least some of the Pleistocene extinctions is that they occurred through habitat changes resulting from the loss of these other keystone species. Here we explore the plausibility of this mechanism, using information on sea otters, kelp forests, and the recent extinction of Steller's sea cows from the Commander Islands. Large numbers of sea cows occurred in the Commander Islands at the time of their discovery by Europeans in 1741. Although extinction of these last remaining sea cows during early years of the Pacific maritime fur trade is widely thought to be a consequence of direct human overkill, we show that it is also a probable consequence of the loss of sea otters and the co-occurring loss of kelp, even if not a single sea cow had been killed directly by humans. This example supports the hypothesis that the directly caused extinctions of a few large vertebrates in the late Pleistocene may have resulted in the coextinction of numerous other species.

Steller's sea cow | extinction | sea otter | Commander Islands | kelp

Explanations for the sudden extinction of more than half of the New World's megafauna at the Pleistocene/Holocene transition is a topic of long-standing interest and debate. Argument has focused on the relative importance of two would-be causes: rapid environmental change associated with late Pleistocene glacial recession, and the effect of early humans crossing Beringia and spreading into the New World. The absence of extinctions in the New World during earlier interglacial periods, together with discovery of similar large-animal losses after the peopling of various other continents and islands, but at widely differing times, has cast doubt on climate change as the extinctions' principal cause (1, 2). This reasoning led to the now widely held belief that human impacts figured prominently in megafaunal extinctions worldwide (3, 4).

The intriguing question is just how aboriginal peoples did this. Was the sudden disappearance of so many large animals entirely a consequence of hunting and overexploitation (5, 6), a pandemic from diseases introduced by early humans or domesticated animals they may have brought with them (7), human-induced environmental changes (e.g., as might have accompanied deforestation or burning) (8), or some combination of these processes?

Another possibility, less discussed in the literature on megafaunal extinctions, is that reductions and complete extinctions of directly hunted species may have led to the loss of other species through cascading indirect interactions. Most speculation about such effects has focused on the loss or decline of predators or scavengers that relied on human-depleted prey [e.g., California condors (9) and Haast's eagle (10)]. Although that is one possible pathway to coextinction, there are others. Ecosystems are

organized around complex interaction webs in which certain species, variously referred to as keystones (11, 12), foundation species (13), and ecosystem engineers (14), can have disproportionately strong influences on population and ecosystem dynamics. Included among these strong interactors are many large-bodied vertebrates (15). Given the abilities of such species to shape the ecosystems in which they occur, it is possible that loss of one or more species by direct human exploitation led to ecosystem changes that in turn caused the demise of multiple other species. Although there has been conjecture that such losses could have significantly contributed to the Pleistocene extinctions (16, 17), detailed understanding of the ecological roles of now-extinct species makes direct examination of this idea difficult. Nonetheless, reliance of some species on the direct or indirect effects of others in complex natural communities mean that a loss of one species may have led to losses of others (18, 19).

Here we explore an example (that of Steller's sea cow, *Hydrodamalis gigas*) that can help inform this hypothesis for Pleistocene extinctions. This particular case is intriguing and potentially informative because various aspects of the rise and fall of sea cows are reasonably well known; the final step in the sea cows' demise occurred just several hundred years ago, in the presence of modern human observers; and dynamics of the coastal kelp forest interaction web, to which the sea cow was intimately linked, have been extensively studied and are well understood. Although aboriginal people (and early Russian fur traders in the Commander Islands) exploited sea cows and may have reduced or even exterminated local populations through that process, humans also hunted and reduced sea otter populations to such low levels that the otter's keystone role in maintaining the kelp forest ecosystem (20) was lost (21–23). Sea cows lived in kelp forests and fed on kelp, thus raising the question of the relative importance in driving the sea cow's demise of the direct effects of human exploitation vs. the indirect effects of reduced food or altered habitat caused by the ecological extinction of sea otters.

Significance

Human-caused extinctions are normally thought to result from overexploitation or habitat alteration. A third possible cause of extinction is the loss of interactions associated with keystone species. Using recent and historical information on sea otters and kelp forests, we show that the extinction of Steller's sea cow from the Commander Islands in the mid-1700s would have been a nearly inevitable consequence of the overhunting of sea otters, which occurred a decade earlier.

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In this article, we use historical records of sea otter harvest from the early maritime fur trade, the functional relationship between sea otter density and kelp abundance, and data on the demographic and behavioral responses to food shortages of dugongs (the sea cow's closest living relative) to argue that the sea cow's extinction in the Commander Islands would have almost inevitably occurred without a single direct human take of the species. We discuss the broader ramifications of this finding to the extinction of sea cows elsewhere in the North Pacific and to extinctions of other large vertebrates after the peopling of the world.

Results and Discussion

Steller's Sea Cow. Hydrodamalines sirenians, which included Steller's sea cow as the last surviving species, radiated from the tropics to coastal waters of the North Pacific Ocean with the onset of late Cenozoic polar cooling (24). On the basis of their cranial morphology (24) and Steller's direct observations (25), sea cows are thought to have been obligate algivores, feeding largely on the diverse and highly productive kelps (order Laminariales) that appear also to have originated or at least diversified in the North Pacific with late Cenozoic polar cooling (26). Steller's sea cow ranged across the Pacific Rim from the northern Japanese archipelago to the Pacific coast of Baja California, Mexico (24), a distribution that was roughly coincident with those of both sea otters and kelps. Sea cows, however, disappeared from most of this region sometime between the Pleistocene and the arrival of the first European explorers to the North Pacific region in the 18th century. The Commander Islands, where an abundance of sea cows survived in 1741 when the Bering Expedition shipwrecked and overwintered there (25), is a notable exception to the sea cow's earlier extinction across the remainder of its range.

Aboriginal humans colonized the Aleutian archipelago by dispersing westward from the New World and inhabiting the more westerly islands at increasingly later times (27). Numerous midden sites attest to a sustained presence of these early peoples on nearly every island of sufficient size. Because of their great distance (>400 km) from Attu Island, westernmost of the Aleutians, the Commander Islands may never have been discovered by New World aboriginals. While artifacts of aboriginal people have been found in association with the Bering expedition's camp site (28), the absence of both living human populations at the time of Bering's shipwreck in 1741 and the lack of midden sites in the Commander Islands suggest these islands were neither permanently occupied nor regularly visited.

The fact that sea cows disappeared from those segments of their historical range that were peopled with aboriginals but survived in abundance at the one location that was not (the Commander Islands) argues for human impacts and against climate change as the principal cause of the sea cow's contraction to a tiny fraction of its former range. With ensuing growth of the North Pacific maritime fur trade, the last sea cow had disappeared from the Commander Islands by 1768 (29).

Exactly how did humans exterminate these last sea cows? The simplest and most straightforward explanation is overkill: rampant exploitation of a behaviorally naive prey by a novel and highly effective human predator. Although sea cow flesh was reportedly delicious (25), and sea cows seemingly would have been vulnerable to human hunters, Anderson (30) proposed that the sea cow's decline and extinction was either caused or helped along by the ecological extinction of sea otters and the resulting collapse of the sea otter–sea urchin–kelp trophic cascade (20). Supporting this possibility is the commonness of starvation in driving periodic rapid declines of many large mammal populations (31) and Steller's observations that over the winter months of low kelp growth, sea cows frequently appeared emaciated (29).

Because it occurred so recently, the extinction of sea cows in their final stronghold, the Commander Islands, provides a possible “Rosetta Stone” (32) for the broader question of how likely

extinctions of past megafauna as a result of indirect community effects really is. Turvey and Risely (33) concluded from a population viability analysis that the extinction of Steller's sea cows in the Commander Islands was an inevitable consequence of human exploitation; the pre-exploitation size of this remnant population was larger than Stejneger's (29) often-cited estimate of 1,500 individuals, and contrary to proposals by Anderson (30) and others, “environmental changes caused by sea otter declines are unlikely to have contributed to this extinction event.” We agree that direct human hunting of sea cows occurred and may well have figured prominently in the sea cow's extinction. However, it is not possible to establish a link between sea cow mortality and human hunting. The mere presence of overwintering fur hunters in the Commanders does not demonstrate that these people were substantially exploiting sea cows [although they surely did some of this (29)], much less the number of sea cows they may have killed and eaten. Direct human effects are thus likely, but not inevitable. Conversely, Anderson's (30) proposal is backed up by compelling evidence: kelp forest collapse after the loss of sea otters is a virtual certainty. The timing of sea otter exploitation and the sea cow's loss on the Commander Islands has led us to believe that the sea cow's extinction from these islands would have occurred as an indirect effect of removing sea otters, even if no direct hunting of sea cows had occurred or it was of minimal importance. In the following sections, we provide data, analyses, and arguments to support our hypothesis.

Kelp and Sea Cows. Kelps and other fleshy macroalgae (hereafter collectively referred to as “kelps”) provide the majority of production to coastal marine ecosystems in the North Pacific Ocean (34). Various and sundry evidence suggests that kelp was also the sea cow's primary food source. First, all extant sirenians are obligate herbivores, and extinct species probably were as well (24, 35–37). Second, macroalgae are the only autotrophs that would have been accessible to sea cows in sufficient amounts to support viable populations. Sea cows could not possibly have subsisted on terrestrial plants or phytoplankton. Seagrasses (*Phyllospadix* and *Zostera*), the only remaining group of autotrophs that might have provided food for sea cows, do occur in some areas of the North Pacific but are rare or absent throughout much of the sea cow's northernmost range, including the Aleutian and Commander islands. Third, loss of dentition and development of a keratinous palatine plate suggest a transition in diet from siliceous sea grasses by primitive tropical dugongids to nonsiliceous macroalgae by hydrodamalines as they radiated into the North Pacific (24). Finally, while shipwrecked on Bering Island during winter and spring of 1741–1742, Steller (25) observed sea cows feeding on kelp.

Sea Otters and Kelp in the Western Aleutian Islands. A trophic cascade in which predation by sea otters limits herbivorous sea urchins is essential for the maintenance of kelp forests across much of the North Pacific Ocean's rocky reefs at higher latitudes (20, 21, 38, 39). Kelp density and standing biomass (a reasonable surrogate for sea cow carrying capacity) is >10-fold lower at islands where sea otter populations have been reduced or lost compared with otherwise similar islands where sea otters abound (21, 40). Moreover, transitions between kelp-dominated and deforested ecosystem states with varying sea otter densities occur rapidly, as sharply punctuated phase shifts (41, 42).

The equilibrium population density for sea otters in the central and western Aleutian archipelago is about 12–15 individuals·km⁻¹ of shoreline, and the breakpoint density of sea otters for the transition from a kelp-dominated to deforested state is about 6 individuals·km⁻¹ of shoreline (43). Hence, a reduction in sea otter abundance below this ecologically effective population size (sensu ref. 44) would have rapidly and profoundly reduced the environmental carrying capacity for sea cows (*K*). The important

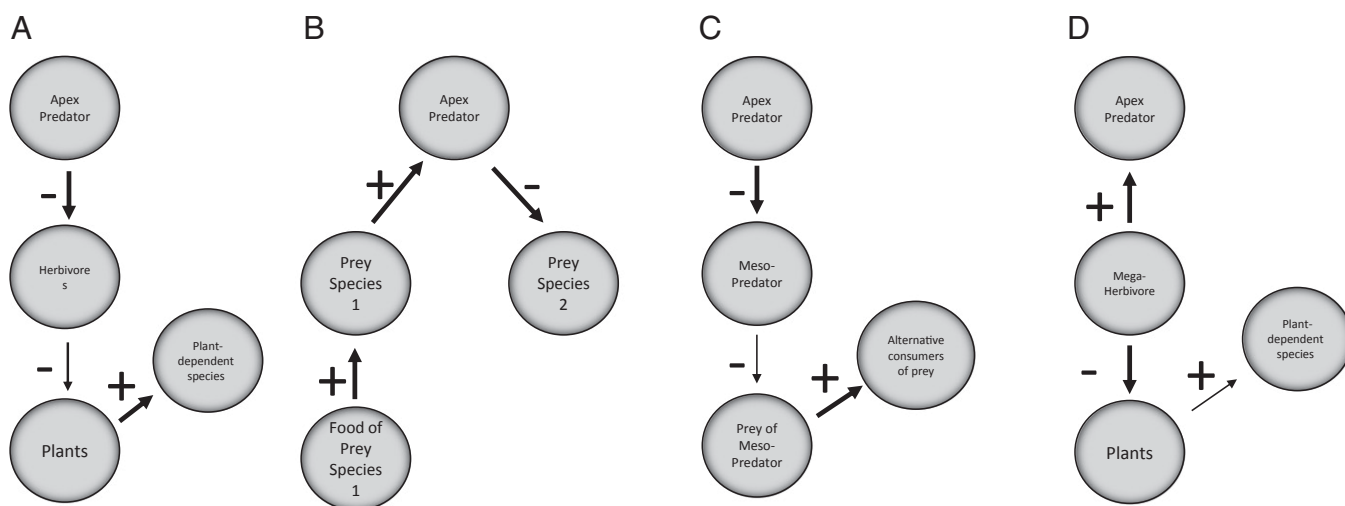


Fig. 3. Some known food web pathways by which changes in abundance of predators and other large vertebrates influence the abundance of other species through indirect interactions involving top-down forcing. (A) Classic trophic cascades. (B) Apparent competition. (C) Mesopredator release. (D) Trophic cascade beginning with megaherbivores and with megaherbivores sustaining predators via scavenging. Arrow line weights correspond with interaction strengths. Extinctions might occur as a result of increased interaction strength at any of the negative linkages. See text for examples.

by applying the demographic and behavioral responses of dugongs (*Dugong dugong*), the sea cow's closest living relative, to catastrophic food loss (51), using simple age-structured population models and general sirenian demographic rates (33, 52). In making projections, we accounted for uncertainty in both life history and rates of starvation-induced mortality. Starvation-induced increases in mortality and cessation in reproduction are predicted to have resulted in rapid declines in a sea cow population (Fig. 3). Starting with 1,500 sea cows at stable stage distribution in 1750 and averaging across all life history and starvation-caused mortality rates, the models predict a mean of one surviving animal by 1768, the year of the recorded extinction; the median number of survivors is zero, and the maximum is six.

We also ran simulations to ask what annual starvation mortality rate would be needed to predict a median of one survivor in 1768; this would be a mortality of 31%, which is considerably lower than any of the direct estimates for mortality in the face of starvation we made from dugong data (50). Furthermore, these effects do not include sea cow emigration. As Preen and Marsh (51) show, dugongs readily move when faced with starvation, and this emigration can account for the majority of immediate local dugong declines. Oral tradition of Aleuts on Attu island (425 km east of Bering Island) states that sea cows were present and being hunted after their extinction on Bering Island (archived notes by L.M. Turner, recounted in ref. 53), thus supporting the possibility that some movement of animals away from Bering Island, their supposed last population, may have occurred. Sea cow bone fragments from the western Aleutian Islands and dated to the past several millennia also may be from Commander Island's emigrants (53).

Conclusions

Using our knowledge of sea otter–kelp forest interactions in the nearby western Aleutians and data on the demographic and behavioral responses of dugongs to food reduction (51), we show that sea cows around Bering Island would have reached near or complete extinction by or very close to 1768, the year of the last reported sighting of a living sea cow (29). Human hunting clearly occurred and may have been largely responsible for the sea cow decline at Bering Island. However, our analyses suggest that the sea cow's extinction from this last stronghold also was a nearly inevitable consequence of the loss of sea otters and kelp forests

and would have occurred without any loss of sea cows to human hunting.

Whether similar ecological processes led to the extinction of Steller's sea cows elsewhere in the North Pacific is more speculative. Aboriginal peoples inhabited all such areas for long periods of time, and the exact timing of the sea cow's disappearance from these areas is unknown. There is evidence that aboriginal humans exploited sea otters, thus driving coastal reefs to the urchin-dominated phase state (23), and few sea cow bones have been recovered from midden sites anywhere (53). However, sea otters were sufficiently abundant throughout this range to support a lucrative fur trade, thus implying that kelp forests were abundant as well. All we can infer with reasonable certainty is that aboriginal peoples and sea cows did not coexist when these peoples were first encountered by western civilization.

Other megafauna, especially large predators and megaherbivores, have comparably important ecological influences to those of sea otters on their associated ecosystems (15, 54, 55). As some of these keystone species were depleted or lost to early peoples, the loss of their community effects may have dragged other species down as well, just as we have proposed for the coextinction of sea otters and sea cows. If some of these other species were also keystones, the process of megafaunal extinction might have progressed rapidly as an ecological chain reaction, thus obviating the need to attribute all or even most of these massive losses directly to humans or a changing climate. The possibility is at least worth further consideration.

Whereas the mechanisms of prehistoric extinctions are difficult to disentangle from paleontological and archaeological records, coextinctions associated with the loss of large vertebrates are known or suspected in modern ecological studies, and can be generated from a variety of ecological effects (Fig. 4). For example, local extinctions of birds and other small vertebrates followed the loss of coyotes from chaparral habitat fragments in southern California (56), a result of increased mortality from mesopredators that grew into coyote-free environments (Fig. 4C). The small vertebrate losses that accompanied mesopredator release in turn may have driven declines of other predators that depended on these small vertebrates for food. Ripple et al. (57) hypothesized one such chain of events, with extirpation of wolves in the northern United States causing increased coyote numbers, thus purportedly forcing snowshoe hare populations downward

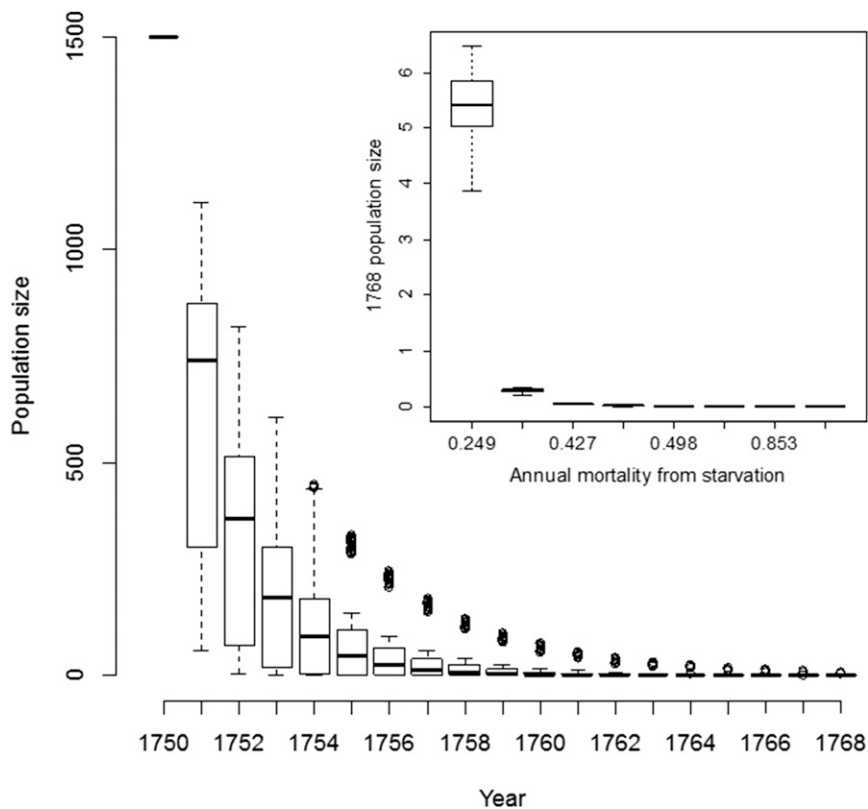


Fig. 4. Modeled sea cow population trajectories in response to kelp forest phase shift after the ecological extinction of sea otters in the Commander Islands. Main figure shows boxplots for the number of living sea cows each year after the onset of starvation, including variation across both estimated starvation-caused mortality rates and life history parameters. (*Inset*) Boxplot for the number of living animals predicted to remain in 1768, the year of the historically recorded extinction, segregated by the assumed starvation-caused annual mortality rate. Only simulations using the lowest of the eight mortality rates predict more than one survivor by 1768, and even this most optimistic scenario always predicts fewer than seven survivors by that year. Note that these predictions do not account for emigration, which would likely reduce local numbers far below those caused just by elevated mortality.

and forcing the hare's obligate predator, lynx, to extinction in local areas as well. Elk and moose population increases in the Canadian Rockies (caused in some cases by forest management practices) have elevated wolf densities, in turn driving caribou numbers downward (58) (Fig. 4B). The loss of wolves, pumas, and grizzly bears caused reductions or losses of various plant, invertebrate, and small vertebrate species from certain riparian habitats in the North American intermountain west (59, 60), a direct consequence of overgrazing by the elevated numbers of large ungulates (in the case of plants) or the knock-on effects of plant reductions (in the case of the various animal species). Other indirect interaction web pathways of obligate relationships between large predators and co-occurring species have been proposed, and still others that may well exist in nature have not yet even been imagined. As our analyses demonstrate, these chains of interactions can be powerful enough to cause significant changes in the abundance of other species, including extinctions. Although similarly detailed knowledge of community interactions are lacking for Pleistocene communities and their many now-extinct species, consideration of such chains of effects should be given when judging the likelihood of overkill as a mechanism that could have generated the wide-ranging extinctions seen wherever human hunters entered novel habitats as they spread around the globe.

Materials and Methods

Much of this article is based on a reanalysis and synthesis of published data from our studies of sea otters and kelp forests in the western Aleutian Islands. We have documented the influences of sea otters on coastal ecosystems by measuring changes that occurred with the recovery of local populations from the Pacific maritime fur trade (21), and then with the more recent collapse of recovered sea otter populations because of killer whale predation (47).

Sea otter populations were surveyed by counting animals from a skiff run parallel to shore. Methodological details are reported by Doroff et al. (48) and Estes et al. (43). Reported trends in sea otter abundance are based on

these survey data, except for the mid-1700s population trend at Bering Island, which is taken from ref. 45.

Sea urchin and kelp abundance was measured in 0.25-m² plots, randomly placed on the seafloor at randomly selected locations along the perimeter of islands with concurrently measured sea otter densities. Methodological details are reported by Estes and Duggins (21) and Watson and Estes (39).

Existence of distinct phase states (kelp forests vs. deforested sea urchin barrens) in the Aleutian archipelago was inferred from cluster and discriminate function analyses of the joint sea urchin/kelp abundance measurements at islands and times where sea otter densities ranged from zero to about 16 animals·km⁻¹ shoreline (43). The functional relationship between sea otter density and reef phase state was determined by logistic regression (see ref. 43 for details).

To project sea cow population responses to kelp reductions that followed the loss of sea otters, we first used the demographic values applied to sea cows by Turvey and Risley (33) and second, we used values for a general sirenian life cycle proposed by Heinsohn et al. (52) in their dugong population viability analysis. We also created 100 random versions of the Turvey and Risley life history, following them in drawing life history values from normal distributions. We also generated all 36 alternative sets of vital rates for the Heinsohn et al. model, based on their maximum and minimum values for the three vital rates (other than interbirth interval) they varied. For each model, we then adjusted interbirth interval to yield a stable population and used the stable age distribution of the resulting model, applied to a total population of 1,500 animals, to initialize simulations of starvation effects. We assume sex-independent survival.

To simulate the effects on sea cow numbers of the loss of kelp forests after sea otter harvest, we require some estimate of starvation-caused mortality. Although we have no data on sea cows and their reactions to rapid declines in their food (kelp), we use documented effects of rapid food (seagrass) losses on dugongs (51), the sea cow's closest living relative. After catastrophic loss of a formerly abundant food source, Preen and Marsh (51) document three responses: movement out of the affected area, near-cessation of reproduction, and dramatically increased mortality. To estimate survival over this starvation event, we used the estimated starting numbers in the most intensively influenced area (1,753 animals) and in a wider area (2,206 animals), in combination with estimates of dugong numbers both immediately (71 and 1,106) and more than a year after the event (257 and 604, respectively, for the smaller and larger areas). The resulting survival rates are

0.041, 0.147, 0.501, and 0.274. The last two estimates of survivor numbers are likely to include most survivors, who moved back to the affected area (51), but we also used another set of estimates, assuming that a substantial number of survivors did not return, and thus those mortality rates were only half the base estimates (survival equal to 0.520, 0.573, 0.751, and 0.637). We multiplied these eight probabilities of surviving starvation with the natural age-dependent survival rates in each of the 236 alternate demographic descriptions and also stopped all reproduction (as reported by ref. 51 for dugongs and conforming to reactions of most large mammals to severe

food shortage) to estimate the rate at which a sea cow population would decline in the face of severe food shortages. We assumed that increased mortality began in 1750 and continued unchanged into the future. Although continuing lack of adequate food would likely result in rapidly increasing mortality, we conservatively kept the risk of starvation-caused death constant each year.

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