

Steller's sea cow uncertain history illustrates importance of ecological context when interpreting demographic histories from genomes

Alberto A. Campos ^{1✉}, Cameron D. Bullen ¹, Edward J. Gregr ^{1,2}, Iain McKechnie ^{3,4,5} & Kai M. A. Chan¹

ARISING FROM F.S. Sharko et al. *Nature Communications* <https://doi.org/10.1038/s41467-021-22567-5> (2021)

In their recent paper entitled “Steller’s sea cow genome suggests this species began going extinct before the arrival of Paleolithic humans”, Sharko et al.¹ use novel genomic methods to infer the demographic history of this species. Based on a single specimen from the Commander Islands, the authors conclude that the species suffered a single catastrophic population decline approximately 400,000 years ago and was thus already on the verge of extinction well before human arrivals in the Late Pleistocene. Here we suggest their demographic assumptions warrant reinterpretation given the ecological barriers that likely structured sea cow populations along the North Pacific Rim. Our preliminary range simulations suggest that the Commander Is. population may have been physically isolated from others, making it unsuitable as a demographic inference for the entire sea cow North Pacific range. Under these assumptions, Sharko et al.’s findings are more likely indicative of the time since the isolation of this remnant population from the rest of the sea cow range, rather than representative of the population contraction of the species. This perspective highlights the importance of considering historical ecology and paleobiogeography when interpreting genomic data to infer past demographic histories.

Since Li and Durbin² published their milestone paper on the development of pairwise sequentially Markovian coalescent (PSMC) models to infer species demographic histories from a single diploid genome, their approach has become extremely popular with iconic endangered (e.g., giant panda³) and extinct species (e.g., passenger pigeon⁴, woolly mammoth⁵). Although there are significant methodological questions, such as the effects that natural selection can have on vertebrate genomes⁶, and separating population size variation from population structure⁷, we believe this method will contribute in impactful ways to our understanding of species demographic histories, especially given the possibility of using few, or single specimens.

However, to appropriately substantiate assumptions, demographic analyses derived from such models must carefully

consider long-term range fluctuations, as well as ecological and behavioural characteristics that would influence the species’ dispersal, distribution and consequently gene flow dynamics⁸. In this sense, although we were pleased to see these novel genetic methods applied to the demographics of marine megafauna in the North Pacific, particularly to Steller’s sea cow¹, we believe an examination of this species’ ecology and biogeography lends clarity to the interpretation of their results.

The North Pacific-wide presence in the fossil record, the absence of visible physical barriers for dispersal and migration, and the sheer size of Steller’s sea cow (i.e., their whale-like appearance suggesting much greater mobility and navigational ability than they may have possessed^{9,10}), have all contributed to the idea that they existed as one large panmictic population. However, different lines of evidence indicate the existence of ecological barriers that could have significantly altered sea cow dispersal and population structure, including both periodic (e.g., flooding of Bering Strait during interglacials; glacier advances) and permanent reproductive barriers, such as several wide and deep channels separating the Aleutian Islands.

To evaluate the ecological influence the Steller’s sea cow may have exerted over kelp forests around the North Pacific Rim¹¹ we have been preparing updated range maps considering the species glacial and interglacial ranges. These nearshore habitat maps are grounded in the fossil record and guided by bioindicators of kelp habitat, oceanographic data, and various lines of ecological evidence^{9–20} (Fig. 1). Our preliminary range maps indicate that the Commanders population has always been physically isolated from both the population of the Kamchatka peninsula to the West (and the entire Asian mainland population for that matter) and from the nearest source to the East, the Near Islands of the Aleutian chain. Recent reconstructions of Beringia during glacial maxima¹² confirm that in any scenario of sea level fluctuation the Commanders have always been isolated from the Asian mainland and the Aleutians by deep channels.

¹Institute for Resources, Environment, and Sustainability, University of British Columbia, Vancouver, BC, Canada. ²SciTech Environmental Consulting, Vancouver, BC, Canada. ³Department of Anthropology, University of Victoria, Victoria, BC, Canada. ⁴Hakai Institute, Heriot Bay, Quadra Island, BC, Canada. ⁵Bamfield Marine Sciences Centre, Bamfield, BC, Canada. ✉email: al.campos@ubc.ca

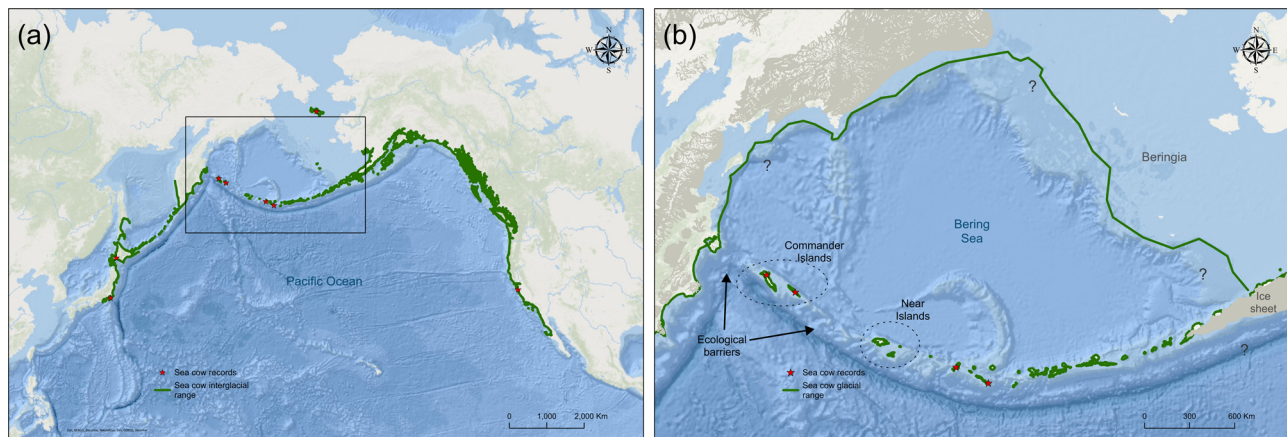


Fig. 1 Steller's sea cow (*Hydrodamalis gigas*) range reconstructions. **(a)** Inter-glacial range. **(b)** Range during glacial maxima. The Commander Islands have always been physically isolated by deep channels - even during lowest sea levels - that likely constituted ecological barriers, or biogeographic breaks, for sea cows. Different lines of evidence (e.g., absence of echolocation or other navigational apparatus¹³; limited ability to submerge⁹; exclusive seaweed diet¹⁰) converge to a strictly coastal, 'linear elongated' distribution along kelp-dominated shorelines, a range that coincided with that of the sea otter, *Enhydra lutris*¹³. Sea cow range reconstructions were based on: (1) review of existing sea cow records (see Dataset); (2) bioindicators of sea cow habitat (i.e., kelp forests, sea otter historical ranges¹⁴); (3) southern extent of winter drift ice and year-round kelp habitat;^{15,16} and (4) the estimated shoreline of Beringia and Bering Sea islands during the Last Glacial Maximum¹². 'Sea cow records' (red stars) refer to undisputed records only. Question marks refer to uncertainties related to sea ice extent along the shoreline of Beringia during glacial times. Map background image source and license: Maps were created using ArcGIS Online basemap 'World Ocean Base' (Esri, GEBCO, DeLorme, NaturalVue) and using ArcGIS® software by Esri. ArcGIS® and ArcMap™ are the intellectual property of Esri and are used herein under license. Copyright © Esri. All rights reserved. For more information about Esri® software, please visit www.esri.com.

Evidence from sea otter morphological and genetic studies¹⁷ has shown population structuring across their range and led to the recognition of different subspecies for the Commander Islands and the Aleutian islands¹⁸ lending support to the idea of ecological barriers at this geographic location. Although we acknowledge considerable differences in life history traits between these species, sea otters are the only other marine mammal restricted to nearshore coastal waters of the North Pacific, sharing a remarkably overlapping distribution with sea cows¹⁹.

The assessments conducted by Krasheninnikov and Steller in Kamchatka and the Kurile Is., supported by interviews with Indigenous Itelmen and Kurile peoples, did not find ethnobiological evidence of living sea cows outside the Commanders, except for anecdotal reports of carcasses washed ashore²⁰. Considering the conspicuousness of the sea cow, this seems to attest to the fact that these animals were hardly, if ever, venturing out of the Commander Is. This is just as we would expect from a strictly coastal sirenian depending on a constant supply of shallow water macroalgae, and possibly freshwater sources^{9,10}. Thus, it does not seem that sea cows were either equipped or enticed to cross the 180 km of deep waters and unsuitable habitat between Bering Island and the mainland (or c.120 km during glacial maxima) without a shoreline to navigate. The 330 km distance between Medny (the easternmost of the Commander Islands) and Attu (the closest of the Aleutian Islands) would have posed an even greater barrier to genetic exchange. Given the predominant oceanographic conditions, it is possible that an occasional vagrant, or a carcass, as mentioned above, could have floated, or been forced by storms or tsunamis from the Commanders to the Kamchatkan mainland. However, the opposite would have been unlikely given the predominant direction of winds and currents and the low probability of a straggler (floating or swimming) from the continent hitting such a small island on the open ocean.

These assumptions have led us to conclude that the Commander archipelago's sea cow population—a notoriously relict, stunted population¹³—has likely been genetically impaired from significant contributions from other regions of the Pacific Rim for

probably most of its history, possibly for as long as it first colonised the islands, except for the occasional immigrant. In light of these possibilities, we believe that the discussions related to the population history of Steller's sea cows made by Sharko et al. may be more relevant if related to the context of the Commander Islands population and its peculiar biogeographic trajectory. At the very least, we argue it is not justified to extrapolate results from a single specimen from the Commander Islands population to the rest of the North Pacific given the uncertainty in when they diverged and the degree to which it was genetically isolated. PSMC models may well be able to provide supporting evidence to address these uncertainties, determining when this founding population first established itself in the Commanders, or help elucidate some of the complex dispersal possibilities discussed above.

Another recent paleogenomic study focusing on Steller's sea cow skin phenotype and cold adaptation has also used PSMC methods to estimate effective population size over time²¹, finding comparable demographic trajectories as Sharko et al. Similarly, since their analyses were only based on individuals from the Commander Islands, their data do not address the question of whether the Commander Islands population accurately represents the demographic history of the species across its former geographic distribution.

Unfortunately, known specimens from outside the Commander Islands are few, and perhaps not able to provide genetic material to allow the level of refinement achieved by Sharko et al. However, the continued development of underwater archaeology and zooarchaeological research may provide future guiding evidence regarding sea cow biogeography and extinction dynamics. In the meantime, similar genetic analyses with existing specimens from California, Alaska (Aleutian and St. Lawrence islands, where other relict populations seem to have persisted through the Holocene) and Japan, may provide a broader perspective on the spatial and demographic dynamics of Steller's sea cow across the Pacific Rim. In any case, ground-breaking methods such as those used by Sharko et al.—when interpreted in the context of

reconstructed species life histories and dispersal dynamics—may constitute one of the best available tools to infer past demographic histories, especially when specimens are rare.

Reporting summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

The data generated in this study, i.e., Steller's sea cow fossil, sub-fossil and recent records, as well as an annotated list of disputed and undisputed records²², have been deposited in the Figshare database under accession code <https://doi.org/10.6084/m9.figshare.19891039.v1>.

Received: 8 September 2021; Accepted: 14 June 2022;

Published online: xx xxx 2022

References

- Sharko, F. S. et al. Steller's sea cow genome suggests this species began going extinct before the arrival of Paleolithic humans. *Nat. Commun.* **12**, 1–8 (2021).
- Li, H. & Durbin, R. Inference of human population history from individual whole genome sequences. *Nature* **475**, 493–496 (2011).
- Zhao, S. et al. Whole-genome sequencing of giant pandas provides insights into demographic history and local adaptation. *Nat. Genet.* **45**, 67–71 (2013).
- Hung, C. M. et al. Drastic population fluctuations explain the rapid extinction of the passenger pigeon. *PNAS* **111**, 10636–10641 (2014).
- Palkopoulou, E. et al. Complete genomes reveal signatures of demographic and genetic declines in the woolly mammoth. *Curr. Biol.* **25**, 1395–1400 (2015).
- Murray, G. et al. Natural selection shaped the rise and fall of passenger pigeon genomic diversity. *Science* **358**, 951–954 (2017).
- Mazet, O. et al. Demographic inference using genetic data from a single individual: Separating population size variation from population structure. *Theor. Popul. Biol.* **104**, 46–58 (2015).
- Pinsky, M. L. et al. Dispersal provided resilience to range collapse in a marine mammal: insights from the past to inform conservation biology. *Mol. Ecol.* **19**, 2418–2429 (2010).
- Steller, G.W. *De Bestiis Marinis. Novi Commentarii Academiae Scientiarum Imperialis Petropolitanae*, Tom. II (St. Petersburg Academy, 1751).
- Steller, G.W. *Journal of a Voyage with Bering (1741–1742)*. 252p. (Stanford University Press, 1988).
- Bullen, C. et al. The ghost of a giant-six hypotheses for how an extinct megaherbivore structured Kelp forests across the North Pacific Rim. *Glob. Ecol. Biogeogr.* (2021). <https://doi.org/10.1111/geb.13370>
- Bond, J. D. *Paleodrainage map of Beringia*. Geological Survey, Yukon Open File 2019-2. (YGS Publication, 2019).
- Domning, D. Sirenian evolution in the North Pacific Ocean. *Univ. Cal. Publ. Geol. Sci.* **118**, 176p (1978).
- Davis, R. W. et al. Future directions in sea otter research and management. *Front. Mar. Sci.*, <https://doi.org/10.3389/fmars.2018.00510> (2019).
- Kenyon, K. *The sea otter in the eastern Pacific Ocean* 366p. (US Dept of the Interior, 1969).
- Crockford, S. J. & Frederick, S. G. Sea ice expansion in the Bering Sea during the Neoglacial: evidence from archaeozoology. *The Holocene* **17**, 699–706 (2007).
- Larson, S. et al. Translocations maintain genetic diversity and increase connectivity in sea otters, *Enhydra lutris*. *Mar. Mamm. Sci.* **37**, 1475–1497 (2021).
- Wilson, D. E. et al. Geographic Variation in Sea Otters, *Enhydra lutris*. *J. Mammal.* **72**, 22–36 (1991).
- Larson, S. et al. The conservation of sea otters: A prelude. In *Sea Otter Conservation* (Academic Press, 2015).
- Steller, G. W. *Steller's History of Kamtchatka: collected information concerning the history of Kamtchatka, its peoples, their manners, names, lifestyle, and various customary practices (1774), English translation. Hist. Transl. Series 12.* 298p. (Univ. of Alaska Press, 2003).
- LeDuc, D. et al. Genomic basis for skin phenotype and cold adaptation in the extinct Steller's sea cow. *Sci. Adv.* **8**, eabl6496 (2022).
- Campos, A. A. et al. Supplementary Data_sea_cow_Campos et al. xlsx. figshare. Dataset. <https://doi.org/10.6084/m9.figshare.19891039.v1> (2022).

Acknowledgements

The authors would like to thank Dr. Benjamin Freeman and Dr. Ana Carolina Meirelles for providing supporting information. This work was supported by a Natural Sciences and Engineering Research Council/NSERC Vanier Canada Doctoral Scholarship (#202011CGV-456849-83624), Ocean Leaders Fellowship, and Society for Conservation Biology Graduate Award (AC); NSERC Canada Graduate Scholarships Master's Program Scholarship, and Ocean Leaders Fellowship (CB); NSERC Discovery Grant 531246 (IM); Ocean Leaders Fellowship, and NSERC Discovery Grant RGPIN-2020-05032 (KC).

Author contributions

K.C. and E.G. conceived of the research; A.C., C.B. and K.C. designed the research, A.C., C.B. and K.C. conducted the research; A.C. prepared the dataset; A.C. and C.B. wrote the manuscript with significant contributions from all authors; and E.G., I.M. and K.C. supervised the research.

Competing interests

The authors declare no competing interests.

Additional information

Supplementary information The online version contains supplementary material available at <https://doi.org/10.1038/s41467-022-31381-6>.

Correspondence and requests for materials should be addressed to Alberto A. Campos.

Peer review information *Nature Communications* thanks Brendan Reid and the other, anonymous, reviewer(s) for their contribution to the peer review of this work.

Reprints and permission information is available at <http://www.nature.com/reprints>

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.



Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons license, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons license, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons license and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this license, visit <http://creativecommons.org/licenses/by/4.0/>.

© The Author(s) 2022