ECOLOGICAL ECONOMICS

Cascading social-ecological costs and benefits triggered by a recovering keystone predator

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Predator recovery often leads to ecosystem change that can trigger conflicts with more recently established human activities. In the eastern North Pacific, recovering sea otters are transforming coastal systems by reducing populations of benthic invertebrates and releasing kelp forests from grazing pressure. These changes threaten established shellfish fisheries and modify a variety of other ecosystem services. The diverse social and economic consequences of this trophic cascade are unknown, particularly across large regions. We developed and applied a trophic model to predict these impacts on four ecosystem services. Results suggest that sea otter presence yields 37% more total ecosystem biomass annually, increasing the value of finfish [+9.4 million Canadian dollars (CA$)], carbon sequestration (+2.2 million CA$), and ecotourism (+42.0 million CA$). To the extent that these benefits are realized, they will exceed the annual loss to invertebrate fisheries (–$7.3 million CA$). Recovery of keystone predators thus not only restores ecosystems but can also affect a range of social, economic, and ecological benefits for associated communities.

As keystone species, top predators can exert strong effects over the function, structure, and diversity of ecosystems (*1*). When these species recover after extirpation, they often reestablish top-down control (*2*) and shift the ecosystem closer to an unexploited state (*3*). This can disrupt social-ecological systems established during the species' absence and lead to conflict between the recovering predator and established human resource users (*4*). Given the widespread defaunation of natural systems (*2*), the societal conflicts arising from such rewilding efforts need to be acknowledged and quantified. However, despite numerous examples of such conflicts (*5*–*7*), the associated social, economic, and ecological changes are rarely documented or evaluated, making it challenging to manage and equitably mitigate impacts.

We demonstrate such an evaluation here by examining the transformation under way in the eastern North Pacific, where sea otters (*Enhydra lutris*), a marine keystone species (*8*), are recovering after near extinction by the maritime fur trade of the 18th and 19th centuries. As predators of invertebrates, in particular kelp-grazing sea urchins, sea otters release kelp from grazing pressure and promote the growth of kelp forests. This increases primary production, fixes free CO_2, and provides vertical habitat for other coastal species, particularly fish (e.g., rockfish, greenlings, and salmon).

This well-studied trophic cascade (*8*, *9*) is broadly seen as a conservation success story and case study in marine ecosystem restoration. However, sea otter recovery is unpopular in many coastal communities where sea otters compete strongly with humans for valuable invertebrates like crabs, clams, and urchins. This has led to conflict with established commercial and subsistence invertebrate fisheries across much of the reoccupied sea otter range. The scope of human-induced sea otter mortality is largely unknown, but may be a factor in slowing range expansion (Fig. 1). Although this conflict was anticipated (*10*, *11*) and reduced invertebrate catches are regularly reported by fishers, the associated costs and potential benefits of sea otter recovery have not been quantitatively assessed (*12*).

Understanding the costs and benefits arising from different ecosystem states is central to effective and equitable resource management. Accordingly, assessments of ecosystem services trade-offs are increasingly common (*13*). However, modeling the complexities of social-ecological systems requires many simplifying assumptions (*14*), which foreclose on our ability to comprehensively assess the full range of values that matter to people (*15*). Different representations are thus necessary for different applications. For example, the literature has focused largely on economic valuation of ecosystem services (*16*, *17*), whereas ecosystem-based management of fisheries has focused on ecological interactions and indicators related to fisheries (*18*, *19*), ecosystem health (*20*), and biodiversity (*21*, *22*). Calibrating relevant indicators with empirical data (*23*) at a scale that accurately represents the system of interest (*17*), articulating them in a way that is informative to management (*24*), and effectively communicating uncertainty (*14*, *25*) remain considerable challenges. Here, to support adaptive resource management, we translate local studies into a regional assessment of four diverse ecosystem services and propose an intuitive and comprehensive method for representing uncertainty. We examine whether sea otter–induced changes in finfish catch, carbon sequestration, and tourism offset the associated acute and contentious economic losses to invertebrate fisheries. These services are all closely linked to the sea otter–induced trophic cascade.

Although our empirical results represent one region, they are representative of these effects across the sea otter range, with some variability (see supplementary materials). More broadly, our interdisciplinary approach of translating field studies into economic value using integrated models, with defensible and intuitive treatment of uncertainty, is broadly relevant across many social and ecological contexts.

We take advantage of a natural experiment under way in Pacific Canada, where sea otters have been reoccupying large parts of their historical range for several decades [(*9*); Fig. 1]. Using a trophic model calibrated with local data, we estimate—with uncertainty—the regional change in biomass resulting from the transformation of an ecosystem without sea otters to one with sea otters present. We then estimate the potential change in value of the four ecosystem services using data on fisheries catch and landed value, tourism choices, carbon pricing, and estimates of trophic transfer efficiency. We also consider how this transformation influences less quantifiable benefits to the broader coastal ecosystem and the nonmonetary services provided to coastal communities. We examine the parametric uncertainty in both the trophic model and the translation of system biomass into economic benefits. Predictions of biomass change are presented showing the range of values under different parameterizations. Uncertainties in the dollar value of the four ecosystem services are presented with credibility estimates intended to show the range of defensible values for each service (see supplementary materials for details).

Our model reproduces observed aspects of the trophic cascade, including the decline of valuable invertebrate species such as geoduck clam, Dungeness crab, and sea urchin and increases in kelp abundance, primary production, and the biomass of lower trophic levels (Fig. 2). The aggregate change in predicted ecosystem

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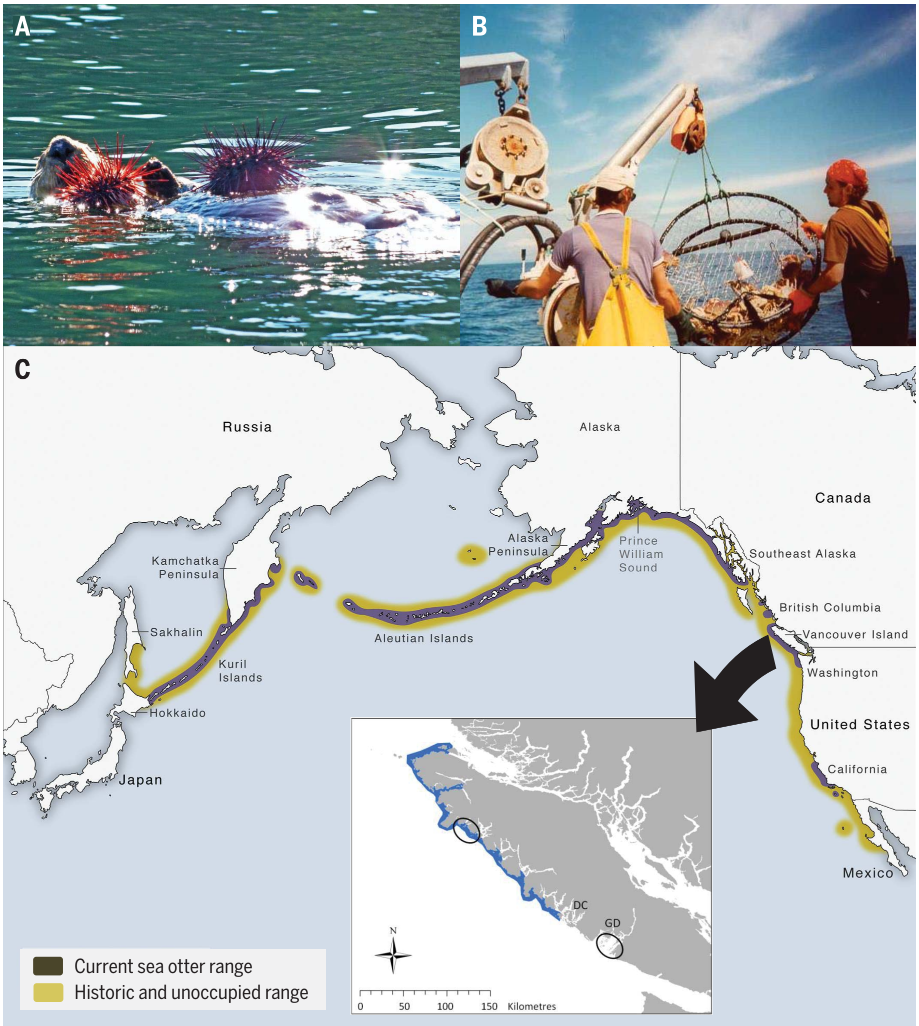

Fig. 1. Ecological and geographic illustration of the study system. (**A**) Sea otter with urchins, a favorite prey item. [Photo credit: B. Nelson] (**B**) Catch of Dungeness crab, a threatened resource. [Photo credit: J. Rogers] (**C**) Range map of historic (yellow) and present-day (dark gray) extents of sea otter distributions in the North Pacific. The inset shows the sea otter range (blue) within the study area, where field data were collected in otter-present and otter-absent areas (ovals), and the location of lucrative Dungeness crab (DC) and geoduck clam (GD) harvesting regions. [Credit: Range map reprinted from (*52*) with permission from Elsevier]

biomass (+37%) reflects the difference between otter-absent and otter-present sites across all groups. Predicted values are reported as median [5th percentile, 95th percentile].

We estimate the lost landed value to commercial invertebrate fisheries from sea otter recovery at 7.3 [4.6, 10.3] million Canadian dollars (CA$)/year (Fig. 3 and table S6). A decline of 25% in the geoduck clam catch comprised over half of this loss. The remainder included the loss of the crab and sea urchin fisheries and a 28% reduction in value to the Manila and butter clam fishery (table S7).

Social and ecological feedbacks (*26*) may mitigate this predicted loss. For example, the global demand for high-value seafood like geoduck clam and Dungeness crab means any reduction in biomass may lead to higher prices, offsetting some of the economic impact to producers. Further, although Dungeness crab largely disappear from our modeled otter-present system, their habitat extends well below the foraging depth of sea otters (*27*). Thus, although lucrative crab fishing grounds in shallow waters will be lost, commercial crab fishers are likely to adapt by shifting fishing efforts to deeper waters.

On the benefits side, costs to the existing fishery are partially offset by a threefold increase in the predicted catch of lingcod, an economically and culturally valuable upper trophic level finfish (Fig. 2 and table S7). More importantly, the increased biomass of kelps and other lower trophic species not explicitly consumed in the model (Fig. 2 and table S8) can yield benefits through deep-ocean carbon storage (*27*) or as a nutritional subsidy to other parts of the ecosystem (*28*, *29*). We estimated the value of this subsidy based on a predicted increase in higher trophic species (i.e., commercial finfish), to be worth 9.4 [2.0, 30.4] million CA$/year (table S6). Uncertainties are high for this service (Fig. 3) because the fate of the surplus production, the trophic transfer efficiencies, and the future landed values are not well known. The estimated value of this service does not include the contribution from increased biomass of subcanopy algal species (*28*), other economic benefits (e.g., recreational fishing, kelp harvesting), or the benefits of the nutritional subsidy to the broader food web.

The portion of unconsumed surplus production lost to deep-ocean storage has value as carbon sequestration. We predict a net benefit of 2.2 [0.5, 7.3] million CA$/year for the sequestered carbon based on European Union carbon prices (Fig. 3 and table S6). This is about one-third of the value obtained by scaling results from a comparable study (*29*) to our study area owing to differences in how kelp production was estimated. Our value can thus be considered a conservative estimate (see supplementary materials for details).

Tourism generates the highest predicted increase in value from sea otter recovery. Our analysis suggests that an otter-dominated system will have the potential to generate a 41.5 [20.7, 66.6] million CA$/year increase in tourism revenue based on willingness-to-pay data derived from a choice experiment (*30*) and recent visitation rates (Fig. 3 and table S6). This estimate does not include likely changes in other tourism-related services such as recreational fishing and destination dive tours. The high uncertainty in this estimate is due to variability in future visitation rates and the estimated willingness to pay. Although this result is based on a local study with existing tourism and sufficient infrastructure to support this increase, other regions in the eastern North Pacific also have established (*12*) or developing (*31*) tourism industries that benefit from the presence of sea otters.

Our estimates of the economic impact of sea otter recovery have wide credibility intervals (Fig. 3), reflecting the uncertainties in parameter values. The distributions of predicted biomass (Fig. 2) were created by randomly resampling the trophic model parameters (see supplementary materials) and show the trophic model was robust to parameter variation. Our social-ecological model combined this uncertainty with other uncertainties, the including the valuation of ecosystem services and trophic interactions among species in the coastal ecosystem. These broad estimates of uncertainty, along with the integration of more generalized models and analyses, combine to improve the representativity of the results to the broader eastern North Pacific. Although more thorough than many published ecosystem models (*14*), further explorations of model sensitivity to different structures (e.g., trophic networks, valuation methods) would be warranted to support management decisions. Such work must face the challenge of the many poorly understood aspects of social-ecological systems (e.g., nonmonetary values, unknown interactions, nonlinear dynamics, and nonstationarity, including the effects of climate change), which are beyond the scope of the present study.

While acknowledging the limitations of our model, we can be reasonably confident that the otter-present system will yield a higher total economic value, because a net positive outcome is implied across the entire range of the credibility intervals (Fig. 3). This is further supported by empirical evidence showing higher biomass and abundance of many important species in otter-present ecosystems (*9*, *32*–*34*). The uncertainty included in the translation of ecosystem indicators to economic value (see supplementary materials) dominates the uncertainty in the trophic model, as illustrated by the different shapes and credibility intervals for the three services (direct catch, supplemented catch, and carbon; Fig. 3) that depend on the biomass estimates from the trophic model. Our estimates of confidence in the ecological and economic assumptions underlying the service valuations thus provide an intuitive way to visualize the uncertainties associated with such transformations. This approach provides a framework for identifying model components that most limit our understanding of social-ecological systems.

We focused here on the four key monetizable services related to the sea otter trophic cascade. However, such transformations are not valued in a strictly monetary sense by coastal communities (*35*), where social and cultural values are multiple and important (*36*–*38*). Additionally, for coastal communities to benefit from such changes, the resources need to be accessible (*39*, *40*). For example, commercial harvesters generally have the capacity to adapt to shifting resource abundance and distribution, whereas Indigenous or recreational harvesters with more restricted harvesting areas may not be able adapt in the same way. Nor do Indigenous community members necessarily have the ability to access areas (e.g., clam beds) throughout their traditional territories or the capital necessary to take advantage of tourism benefits. Localized losses to subsistence and recreational users can thus be difficult to offset. Given the consolidated nature of invertebrate fisheries in our study area (*41*, *42*) and the relative accessibility of nearshore finfish, the predicted redistribution of biomass from commercial invertebrates to nearshore finfish might be a more equitable distribution of the region's marine productivity. However, the value of tourism, finfish, and invertebrates are not necessarily culturally equivalent to different communities. The benefits of sea otter recovery are therefore likely to be distributed inequitably among economic sectors and local communities, especially of Indigenous peoples, who may experience the losses more acutely than the regional economy as a whole. Although coastal communities in the Pacific Northwest have experienced and adapted to similar shifts in the past (*43*), future adaptation will depend on flexible, multilevel governance structures that allow social-ecological systems to be transformed into more desirable states (*36*, *44*).

Understanding the trade-offs between sea otters and commercial fisheries requires historical context. Today's commercial invertebrate fisheries were made possible by the earlier extirpation of sea otters, which led to hyperabundant populations of large individuals in these target species (*35*), making them an economically viable resource (*5*). The otter-absent system, with its large, abundant invertebrates, thus likely represents a shifted baseline (*45*) for evaluating ecosystem trade-offs, and one that favors the status quo. Nevertheless, the predicted losses to commercial harvesters and coastal communities are legitimate and considerable. Mitigating these social impacts, perhaps by adapting traditional management methods (*36*), could make sea otters less contentious and reduce illegal culling.

Kelp forests also provide additional ecological benefits to the health and productivity of the broader ocean that are outside the scope of our model. Although not yet fully quantified, kelp forests provide habitat to many species and can enhance both biodiversity and resilience (*32*, *46*). The otter-present system would thus seem to support a more resilient social-ecological system, given the increased ecological redundancy and opportunities for diversified fisheries portfolios (*47*).

Further, although our study quantifies the benefits of increased primary production as a nutritional subsidy to one part of the food web (i.e., through catch of valuable finfish), the kelps sustain other coastal species (*48*), as well as pelagic and benthic food webs, because nearly half of the kelp production is estimated to be exported offshore (*49*). How this allochthonous carbon is partitioned between the various food webs and deep-ocean storage remains to be determined. However, it is clear that some coastal regions, including our study area (*50*), export considerable biomass to the open ocean. We therefore propose that kelp-dominated nearshore areas likely serve as primary production pumps and are thus more valuable to

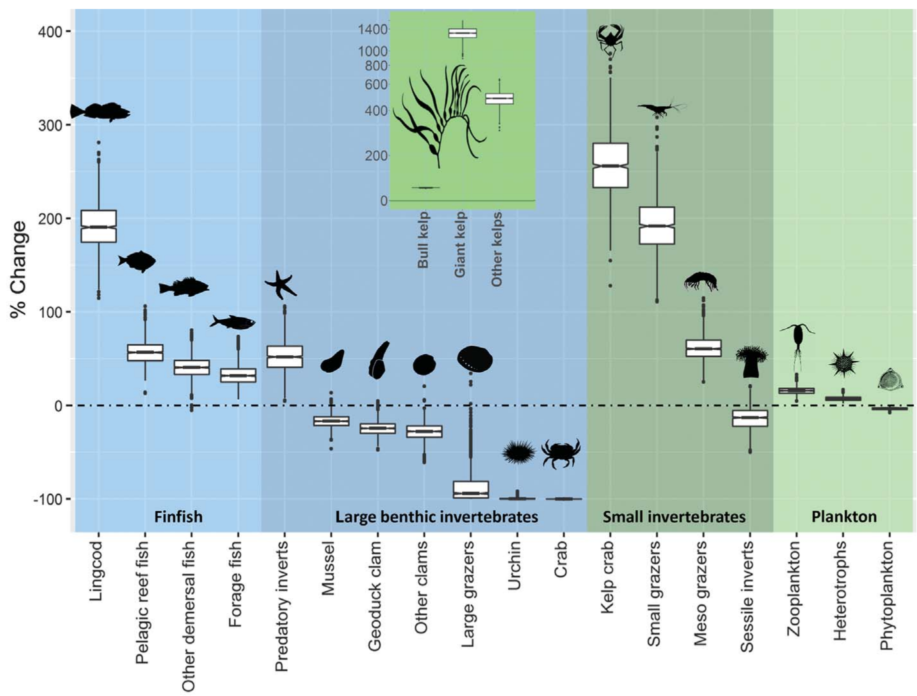

Fig. 2. Percent change in biomass from an otter-absent to an otter-present system. Kelp groups (order Laminariales) are shown as an inset to accommodate the much larger relative biomass change. Functional groups are organized by trophic position (colored background) and then ordered by proportional change, illustrating the switch from a benthic to a more pelagic system and the unaccounted-for surplus biomass in small invertebrates—a key component of the nutritional subsidy to the supplemented catch service (Fig. 3). Boxplots show the range of values resulting from an exploration of valid parameterizations (see supplementary materials for details).

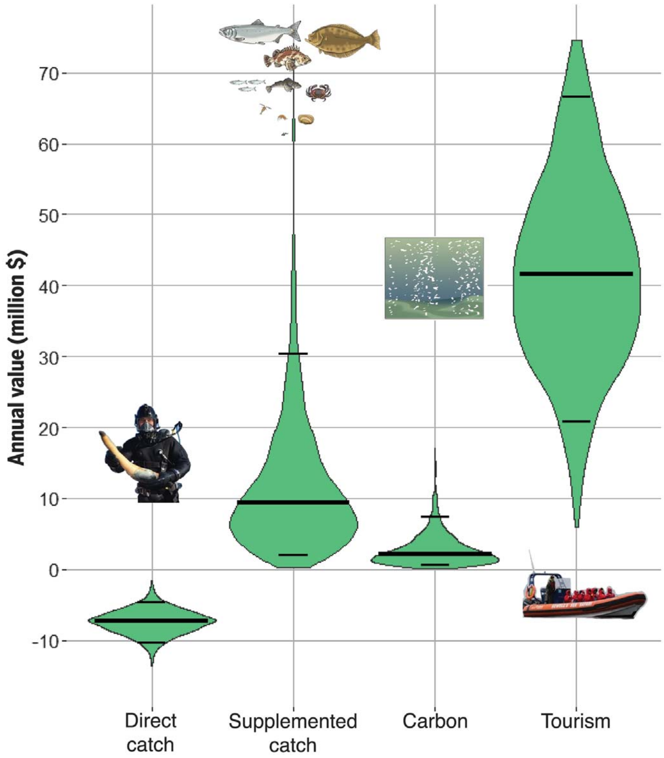

Fig. 3. Sea otter–induced change in annual value for the four ecosystem services considered in this analysis: direct catch, supplemented catch, carbon, and tourism. Changes in value, represented as the difference (in 2018 CA$) between ecosystems with and without sea otters, are shown as violin plots, where the relative widths of the each plot represent the probability distribution of the prediction (like a histogram). The mean and 5th and 95th percentiles are shown as horizontal lines and can be considered the credibility intervals for each service value. These credibility intervals include uncertainties related to the trophic model and in the steps applied to translate the resulting change in ecosystem service supply to dollar values. The intervals reflect the confidence associated with the production and value of each service. Graphical elements illustrate key aspects of each service: Geoduck clams are collected as part of a dive fishery and are the highest value invertebrates in the direct catch; the supplemented catch is defined by a trophic flow to valued finfish such as salmon and halibut (shown at the top of a food chain); marine carbon deposition is principally in the form of marine snow; and wildlife viewing trips are the most conspicuous component of the economic benefits to tourism. [Photo credit: Geoduck diver image provided by the Geoduck Harvesters Association and used with permission]

the world's oceans than previously described [e.g., (*51*)].

The social-ecological model we developed allows the assessment of important social and ecological trade-offs, providing insights into the changes resulting from the recovery of sea otters in the eastern North Pacific. Although the four services we considered (existing invertebrate commercial fisheries, tourism, supplemented finfish catch, and carbon sequestration) do not represent a comprehensive assessment of the social-ecological system, they do provide an innovative perspective on the value of the two ecosystem states. Such integration of diverse services provides a stepping stone toward more complete cost-benefit analyses. Importantly, our broad representation of uncertainty shows how confidence in social-ecological models can be expressed in an intuitive and comprehensible way, allowing meaningful comparisons while illustrating the breadth of uncertainty inherent in such models. Our findings illustrate how sea otters, like many carnivores, exert an oversized effect on social-ecological systems. Hence, coupled social-ecological models are needed for accurately assessing the trade-offs that accompany the loss or recovery of top carnivores in dynamic, continuously adapting systems. Quantifying the impacts of such transformations will inform adaptive management, help mitigate conflicts, promote public acceptance of ecosystem change, and help identify alternate opportunities for local communities.

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ACKNOWLEDGMENTS

We thank the communities of Kyuquot and Bamfield, British Columbia, for their hospitality and the Ka:'yu:'k't'h'/Che:k:tles7et'h' and Huu-ay-aht First Nations for providing access to their territories for this work. H. Eyster produced the species outlines in Fig. 2. These are available through Phylopics. N. Bennett provided valuable insights into the nature of nonmonetary benefits, and C. Bullen's careful review improved the quality of this manuscript. We also thank the four anonymous reviewers whose comments improved both the relevance and reproducibility of this work. **Funding:** E.J.G. was funded by a Canadian Graduate Scholarship (DG 06-5566); K.M.A.C., E.J.G., J.B.S., E.A.P., C.D.G.H., R.G.M., and R.W.M. were funded by a Canadian Natural Science and Research Council Strategic Grant (SPG 08-1970) to K.M.A.C., C.D.G.H., E.A.P., and J.B.S. We also acknowledge a Canadian NSERC Discovery Grant (RGPIN-2015-05105, K.M.A.C.). **Author contributions:** E.J.G., K.M.A.C., C.D.G.H., J.B.S., E.A.P., L.N., R.G.M., R.W.M., and J.C.W. conceived of the study; E.J.G., E.A.P., and V.C. designed the trophic models; R.G.M., R.W.M., J.B.S., E.A.P., C.D.G.H., and E.J.G. collected the data as part of the British Columbia Coastal Ecosystem Services project; J.C.W. and L.N. contributed critical local knowledge and longitudinal data; E.J.G., K.M.A.C., E.A.P., and V.C. conducted the analysis; E.J.G. wrote the manuscript with substantial contributions from all co-authors. **Competing interests:** R.G.M. is currently a marine conservation scientist with, and R.W.M. is currently the owner and operator of, Outer Shores Expeditions, a wildlife and cultural expedition tourism company that operates on the British Columbia coast. **Data and materials availability:** All data are available in the manuscript or the supplementary materials.

SUPPLEMENTARY MATERIALS

science.sciencemag.org/content/368/6496/1243/suppl/DC1
Materials and Methods
Tables S1 to S8
References (*53–111*)
Data S1 and S2

26 June 2019; accepted 5 May 2020
10.1126/science.aay5342

Science

Cascading social-ecological costs and benefits triggered by a recovering keystone predator

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Science **368** (6496), 1243-1247.
DOI: 10.1126/science.aay5342

The benefits of ecosystem restoration

Human activities have fundamentally altered many ecosystems. Recent successful restoration efforts have led to healthier ecosystems, but this has led to a disruption in economies dependent on the altered state of the system. One of the best-known trophic cascades is the sea otter–kelp forest system, wherein recovery of once extirpated sea otters is bringing back biodiverse and healthy kelp forests but reducing the abundance of harvested shellfish. Gregr *et al.* looked at the costs and benefits of this shift and found that for key trade-offs, the value of kelp forest–associated features such as tourism, fin fish fisheries, and carbon capture outweighed the losses to economies (see the Perspective by Estes and Carswell). Thus, ecosystem recovery can benefit both ecosystems and economies.

Science, this issue p. 1243; see also p. 1178

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