

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

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Abstract

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 sea otter presence yields 37% more total ecosystem biomass annually, increasing the value of finfish (+9.4 M\$), carbon sequestration (+2.2 M\$), and ecotourism (+42.0 M\$). To the extent these benefits are realized, they will exceed the annual loss to invertebrate fisheries (-7.3 M\$). Recovery of keystone predators thus not only restores ecosystems, but can also affect a range of social, economic, and ecological benefits for associated communities.

One sentence summary (150 char)

Predator re-introduction can induce ecosystem changes and lead to resource use conflicts, but the cumulative benefits may outweigh commercial losses.

As keystone species, top predators can exert strong effects over the function, structure and diversity of ecosystems (1). When these species recover following extirpation, they often re-establish 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 re-wilding 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 underway in the eastern North Pacific, where sea otters (*Enhydra lutris*), a marine keystone species (8), are recovering after near extinction via 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 CO₂, 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 commercially valuable invertebrates like crabs, clams, and urchins. This has led to conflict with established commercial and subsistence invertebrate fisheries across much of the re-occupied sea otter range. The scope of human-induced mortality is unknown, but may be a factor in slowing their range expansion (Fig. 1). While 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 measurable ecosystem services (16, 17), while 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 significant 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. While 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 underway in Pacific Canada where sea otters have been re-occupying 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 cultural services provided to coastal communities. We examine the parametric uncertainty in both the trophic model, as well as in the translation of system biomass into economic benefits. Predictions of biomass change are presented showing the range of values under different parameterizations, and the 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 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] M CA\$/year (Fig. 3, 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, while Dungeness crab largely disappear from our modeled otter-present system, their habitat extends well below the foraging depth of sea otters (27). Thus, while lucrative crab fishing grounds in shallow waters will be lost, commercial crab fishers are likely to adapt by shifting fishing effort to deeper waters.

On the benefits side, costs to the existing fishery are partially offset by a 3-fold increase in the predicted catch of lingcod, an economically and culturally valuable upper trophic level finfish (Fig. 2, Table S7). More significantly, the increased biomass of kelps and other lower trophic species that is not explicitly consumed in the model (Fig. 2, Table S8) can yield benefits through deep ocean storage (27), or as a nutritional supplement to other parts of the ecosystem (28, 29). We estimated the value of the nutritional supplement, based on a predicted increase in higher trophic species (i.e., commercial finfish), to be worth 9.4 [2.0, 30.4] M 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 value, are not well known. The estimated value of this service does not include the contribution from increased biomass of sub-canopy algal species (28), other economic benefits (e.g., recreational fishing, kelp harvesting), or the benefits of the nutritional supplement to the broader food web.

The portion of unconsumed surplus production lost to deep storage has value as carbon sequestration. We predict a net benefit of 2.2 [0.5, 7.3] M CA\$/year for the sequestered carbon based on European Union carbon prices (Fig. 3, Table S6). This is about 1/3 of the value obtained by scaling results from a comparable study (29) to our study area due 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] M CA\$/year increase in tourism revenue based on willingness-to-pay data derived from a choice experiment (30) and recent visitation rates (Fig. 3, 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. While 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 how the uncertainties in parameter values were represented. The distributions of predicted biomass (Fig. 2) were created by randomly re-sampling 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 including valuation of ecosystem services and potential 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. While 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., unknown interactions, non-linear dynamics, and non-stationarity, 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, as 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 and 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 commercial 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, while commercial harvesters generally have the capacity to adapt to shifting resource abundance and distribution, 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 in the short term. While 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 (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 a hyper-abundance in these target species (35) making them an economically-viable resource

(5). The otter-absent system, with its 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 significant. Mitigating these social impacts, perhaps by adapting traditional management methods (36), could make sea otters less contentious and reduce illegal culling.

Kelp forests likely provide additional ecological benefits to the health and productivity of the broader ocean that are outside the scope of our model. While such effects have yet to be 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, while our study quantifies the benefits of increased primary production as a nutritional supplement 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, as 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 sea 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 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. While 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 a novel perspective on the value of the two ecosystem states.

Such integration of diverse services provides a stepping stone towards 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 over-sized 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 ecological 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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Photo credits: Figure 1a, Russell Markel; Figure 1b, Juanita Rogers, Figure 3, geoduck diver provided by the Geoduck Harvesters Association and used with permission. North Pacific range map in Figure 1 reprinted from (52) with permission from Elsevier.

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Author's contributions: EG, KC, CH, JS, EP, LN, RM, RM, and JW conceived of the study; EG, EP, and VC designed the trophic models; RM, RM, JS, EP, CH, and EG collected the data as part of the British Columbia Coastal Ecosystem Services project; JW and LN contributed critical local knowledge and longitudinal data; EG, KC, EP, and VC conducted the analysis; EG wrote the manuscript with significant contributions from all co-authors.

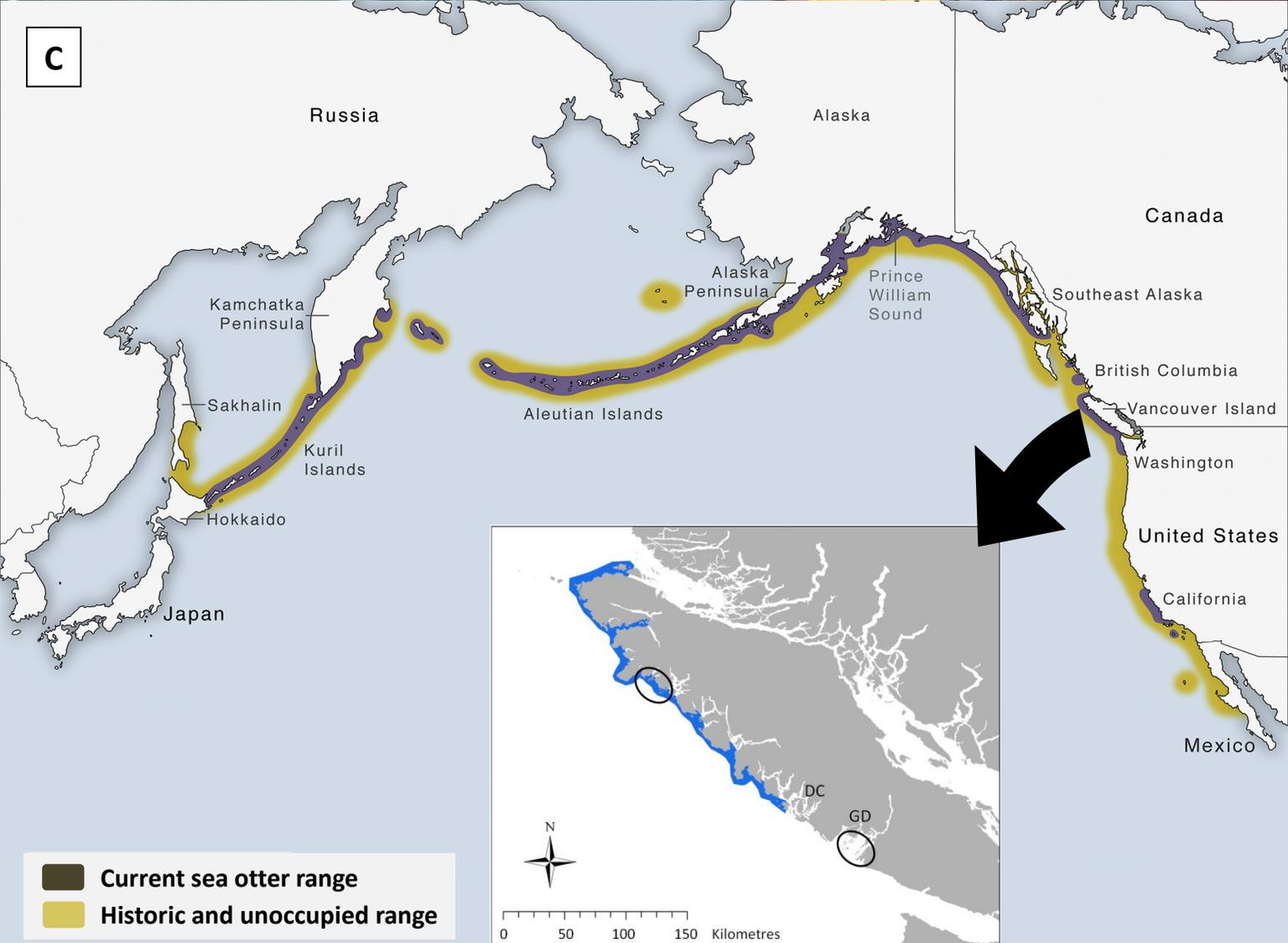
RGM is a Marine Conservation Scientist with, and RM is the owner/operator of Outer Shores Expeditions, a wildlife and cultural expedition tourism company that operates on the British Columbia coast.

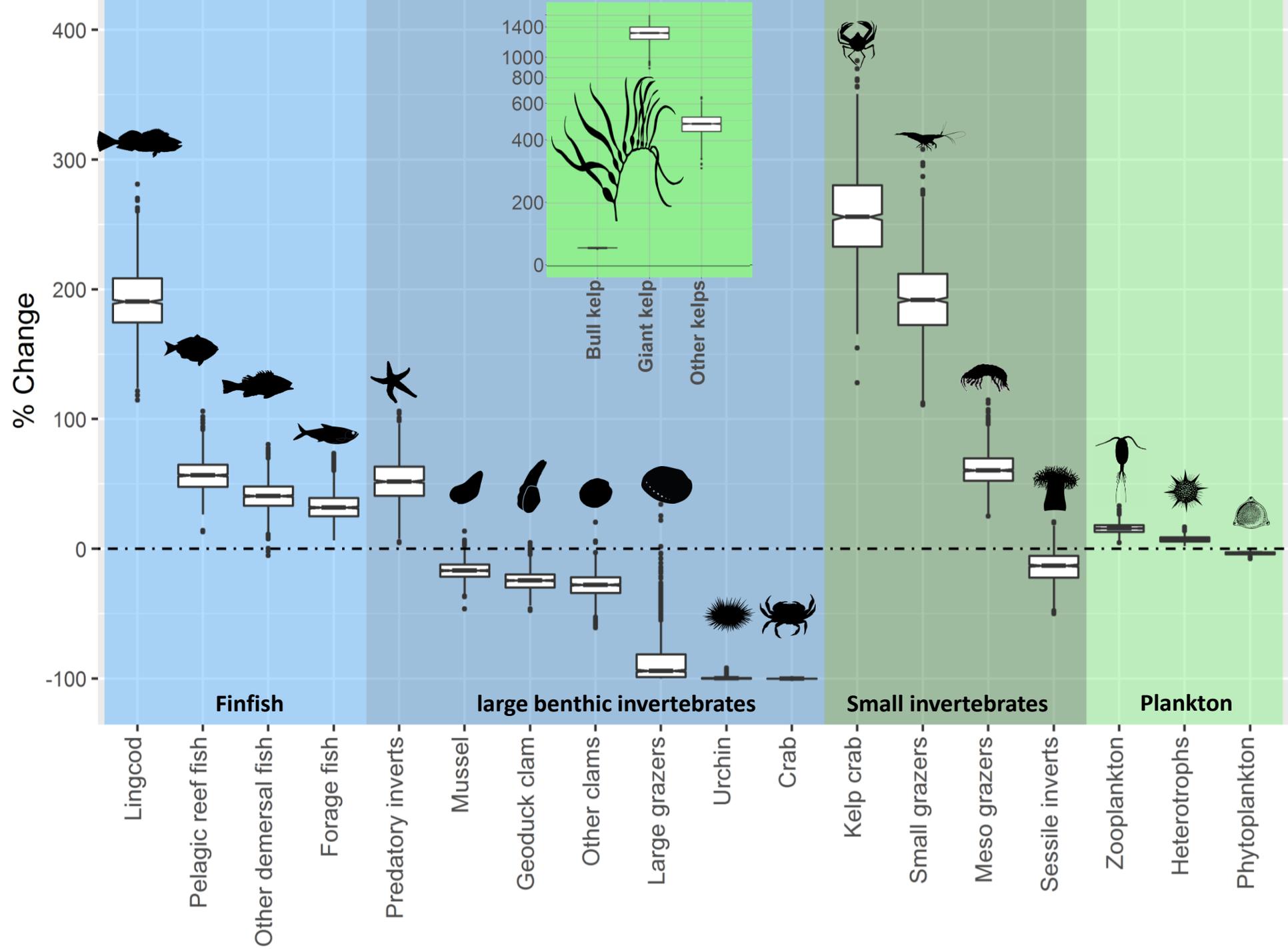
All data are available in the manuscript or the supplementary materials.

Figure 1: Ecological and geographic illustration of the study system. (A) Sea otter with urchins, a favorite prey item; (B) catch of Dungeness crab, a threatened resource; and (C) Range map of historic (yellow) and present-day (dark grey) extents of sea otter distributions in the North Pacific, with inset showing 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 (DG) and geoduck clam (GC) harvesting regions.

Figure 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 and ordered by proportional change, illustrating the switch from a benthic to a pelagic system, and the unaccounted for surplus biomass in small invertebrates - the source of the supplemented catch service (Fig. 3). Boxplots show the range of values resulting from an exploration of valid parameterizations (see supplementary materials for details).

Figure 3: Sea otter-induced change in annual value for the four ecosystem services considered in this analysis. 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 represents the probability distribution of the prediction (like a histogram). The mean, fifth, and 95th percentile 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.





Annual Value (Million \$)

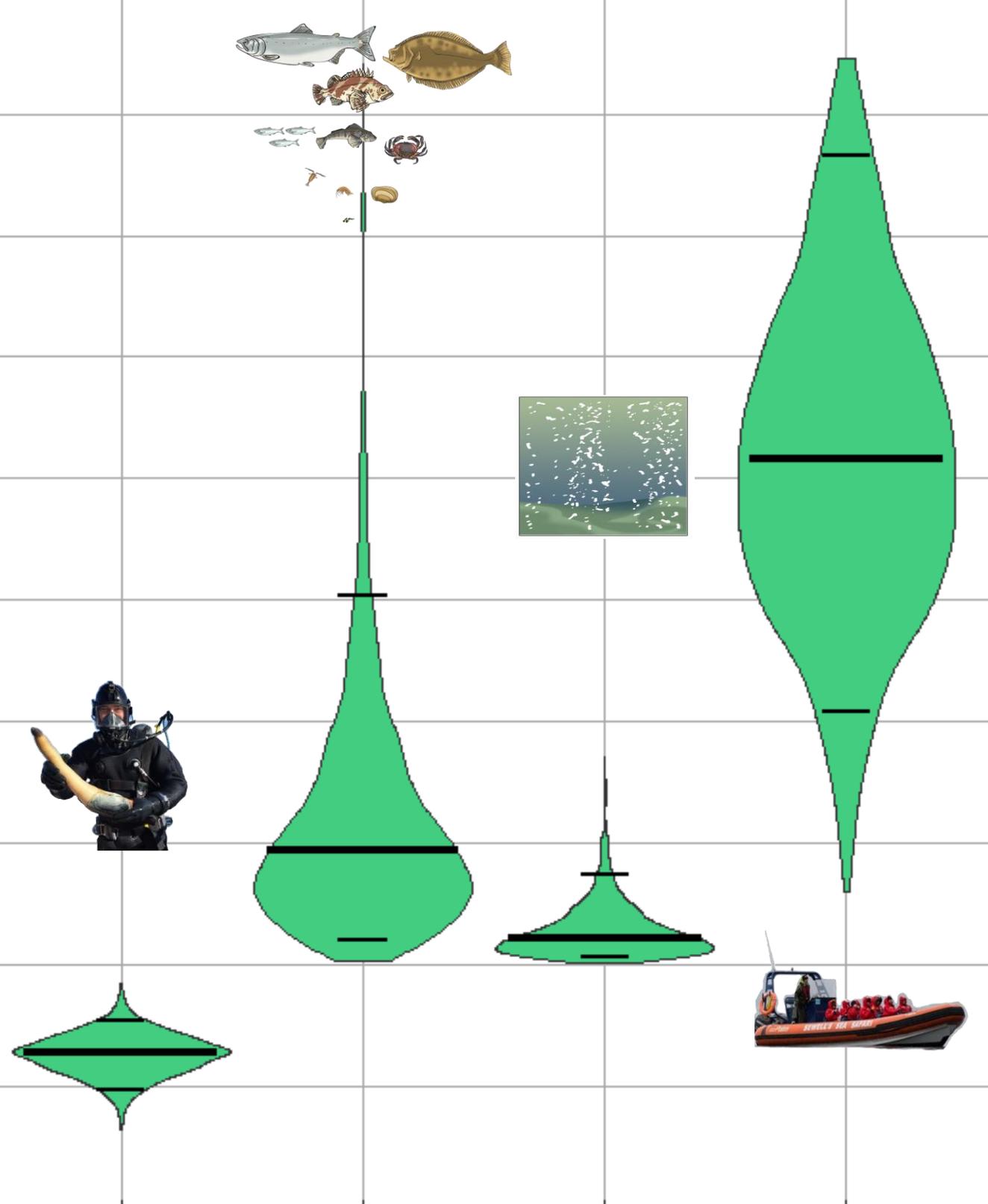
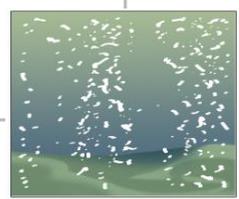
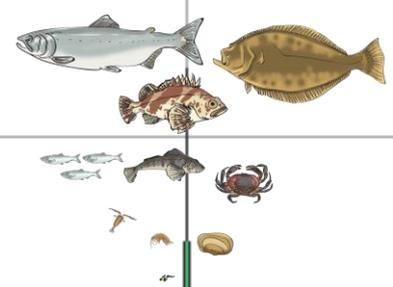
70
60
50
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30
20
10
0
-10

Direct
Catch

Supplemented
Catch

Carbon

Tourism



Direct
Catch

Supplemented
Catch

Carbon

Tourism



Supplementary Materials for

Social-ecological changes triggered by a recovering keystone species

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Table S1. Primary Ecopath parameters. Production (P/B) and consumption (Q/B) rates, local, observed biomass (B, $\text{g}\cdot\text{m}^{-2}$) and proportional change (ΔB) from otter-absent to otter-present systems, B values scaled to the study area for the two sea otter states, and the source of the data. Values in italics were input to the Ecopath model. Biomasses for groups with no values listed in the Scaled-Absent column were estimated using an assumed ecotrophic efficiency (EE). Other model sources are described in the text. Shaded values were used to create the predicted time series used for vulnerability fitting and model assessment. See supplemental materials text for additional details and terminology.

Table S2. Ecopath diet matrix. Predators are shown in columns, and their prey as rows. All columns sum to 1 representing the initial diet of all species groups except lingcod, which import 50% of their diet from outside the model system.

Table S3. Data quality for the main model parameters for each species or group. Each parameter was assigned a coefficient of variation corresponding to its data quality ranking for the re-sampling process (low = 0.80, medium = 0.40, and high = 0.20).

Table S4. Scaled average catch rates for key commercial species. Average and standard deviation of the annual (1983 - 2008) catch of the 5 commercial species explicitly included in the trophic model for Fisheries and Oceans statistical areas 23 through 26. Catches are scaled to a catch rate based on the 4112 km^2 study area. This served as the fishing mortality in the otter-absent Ecopath model. Lingcod was scaled by an additional 0.10 to account for the majority of the catch occurring deeper than our study area.

Table S5. Vulnerability classes. Classification of functional groups into vulnerability classes based on understanding of ecological role and interaction with sea otters.

Table S6. Change in value of modeled ecosystem services. Median change in value (millions of 2018 CA\$) of ecosystem services on the West coast of Vancouver Island due to the transition from a sea-otter absent, urchin dominated system to an otter-present, kelp-dominated system. Predictions include estimates of key uncertainties for each service, shown as the 5th and 95th percentiles.

Table S7. Change in value of commercial fisheries. Change (from otter-absent to otter-present) in annual landed value (millions of 2018 CA\$) of nearshore commercial species on the West coast of Vancouver Island. Landings (in kilotonnes) for the otter-absent state are based on the measured catch rate (Table S4). For the otter-present state, landings are based on the median catch rate from the simulated results. The total difference differs very slightly from Figure 3 and Table S6 because of the resampling applied.

Table S8. Changes in biomass of modeled groups. Relative change (ΔB) in biomass values ($\text{g}\cdot\text{m}^{-2}$) from an otter-absent to an otter-present state by trophic group.

Data S1. Landed weights and values for British Columbia invertebrate and groundfish fisheries (2001-2010). Data compiled from annual seafood industry reviews produced by the British Columbia Ministry of Agriculture (<https://www2.gov.bc.ca/gov/content/industry/agriculture-seafood/statistics/industry-and-sector-profiles>).

Data S2. Visitation rates (2009-2013) to Pacific Rim National Park, British Columbia, Canada. Data compiled in 2015 from Parks Canada online Attendance summaries. These data are no longer available on the Parks Canada website.

Materials and Methods

1. Overview

This study estimated the change in dollar value of a suite of ecosystem services associated with coastal marine systems in response to a trophic cascade triggered by the recovery of the sea otter (*Enhydra lutris*), a keystone species. A model of trophic dynamics was used to estimate the change in biomass for 22 species or functional groups (i.e., groups of functionally similar species) using Ecopath with Ecosim (53). The changes in biomass of these ecosystem service providers from the otter-absent to otter-present state were then used to estimate the dollar value of a suite of relevant ecosystem services.

We developed ecosystem service models to translate ecosystem service provider biomass into four services closely related to the invertebrate fisheries – sea otter recovery context. The main service to consider is the established commercial invertebrate fisheries. We contrast the loss in value of this service to the benefits of a recovered sea otter population, separated into estimates of existence and ecological value. Existence value of sea otters is difficult to measure (15). Here we used tourism as a proxy to estimate the additional cost tourists would pay for their trip to include sea otter sightings. We represented the value of ecological services provided by sea otters by estimating the value of the kelp forests that thrive in their presence. These kelp forests provide a nutritional supplement to marine systems, which we measured by estimating potential increases in commercial finfish. Kelp forests also contribute to carbon sequestration, an alternative, monetizable fate of the carbon captured by the increased kelp production. Details on the valuation models are provided below. All monetary values are reported in 2018 Canadian dollars (CA\$), accounting for inflation but with no discounting.

The change in landed value of existing fisheries was estimated based on recent average reported catch and landed value data and the assumption of consistent catch and pricing (with uncertainty) in the future (details below). It was thus influenced only by a change in the production of valued species. The potential increase in commercial finfish (supplemented catch) was valued by translating estimates of surplus production into valued finfish species, based on estimates of trophic partitioning, transfer efficiency, and present-day value for higher trophic level finfish (e.g., salmon, rockfish, halibut). The value of carbon sequestration was based on estimates of trophic partitioning, and present-day carbon pricing, while the change in tourism value was based on the public's willingness to pay to see otters in the study area. To assess the trade-off between otter-absent and otter-present ecosystems, the total economic losses to coastal fisheries were compared with the value generated from the nutritional supplement to high value finfish, carbon sequestration, and tourism in the sea otter-present system. Several less quantifiable ecological and cultural services influenced by the trophic cascade were assessed qualitatively and are discussed in the main text.

In the sections below, the trophic model is first described in general terms. This is followed by an overview of how uncertainties were handled in both the trophic model and the ecosystem service valuation. The final two sections provide details on the ecosystem service models, and the parameterization of the trophic model.

2. The trophic model

A mass-balanced Ecopath model was developed to represent the otter-absent system using biomass (B , in $\text{g}\cdot\text{m}^2$), production (P/B) and consumption (Q/B) as annual rates. The Ecopath model provides a mass-balance solution to the resulting system of linear equations given by

$$BA_i = B_i * (P/B)_i - F_i - M2_i \times B_i - E_i - M0_i \times B_i$$

where i indexes the functional group, and determines the number of equations in the system. BA is the biomass accumulation rate for group i . An Ecopath model is balanced if the BA values for all groups equals zero. This is the case when the production (P), defined as biomass (B) times the production/biomass ratio (P/B), is balanced by the various loss terms including the total fisheries catch rate (F), the predation rate by other groups ($M2$), net migration (E), and other, non-predation mortality ($M0$). P/B corresponds, under most conditions, to the total mortality as typically estimated from stock assessments. It is thus estimated independently of B , which is a density intended to apply to the entire study area.

Additional terms of interest for model development include the consumption/biomass ratio (Q/B) and ecosystem efficiency (EE), which are components of the predation and the other mortality rates respectively and are defined as:

$$M2_i = \sum_{j=1}^n \frac{Q_j \times DC_{ji}}{B_i}$$

$$M0_i = \frac{P_i \times (1 - EE_i)}{B_i}$$

The predation term ($M2$) links predators and prey by accounting for how much of each prey species or group (i) is consumed by the each of its predators (j). Q_j is the total consumption rate for group j , and DC_{ji} is the portion of predator j 's diet comprised by prey i . Q_j is calculated as the product of B_j and $(Q/B)_j$. As with the P/B ratio, the Q/B rate is independent of the actual B , and is typically estimated as an annual ration. EE represents the portion of a group's biomass that is accounted for in the model, and thus allows for biomass leakage from the model domain. See (53) for additional details on the equations and their solutions.

In this study, the Ecopath model was focused on commercially-fished invertebrate species that are also key components of the sea otter diet, and on the trophically-related species assemblages (functional groups). Commercially important species were included explicitly in the trophic model, and non-commercial species were combined into functional groups, a common practice in ecosystem models.

Field data were collected May through August 2009 on the density and size of kelp and a subset of key kelp-associated species at rocky reef sites in both sea otter-occupied and sea otter-absent regions on the west coast of Vancouver Island, British Columbia, Canada, to estimate species biomass per unit area (B) (Table S1). Data were collected by scuba at 3 sites in Kyuquot Sound, where sea otters had been present for more than 40 years, and 3 sites in Barkley Sound, where sea otters were still absent. All sites had similar wave exposure, substratum, slope, and therefore likelihood of supporting *Macrocystis*-dominated kelp forests. At each site, densities and sizes of large mobile invertebrates (large grazers and predatory invertebrates) were measured along six haphazardly placed replicated 30 x 2 m belt transects separated by 10-30 m at depths of 6-10 m below Canadian chart datum. For large mobile invertebrates, the first 30 individuals were measured and subsequent individuals were only counted. The size distribution of the first 30 individuals was applied to estimate the sizes of unmeasured individuals for each transect. Along the same transects, densities and sizes of canopy kelps and understory kelps and visible small grazers and decapod crustaceans were measured in 16 to 20 replicate 1 m² quadrats. For other small grazers, decapod crustaceans, meso-grazers and sessile invertebrates, 6 replicate 25 cm x 25 cm quadrats were haphazardly placed between 3.3 – 10.9 m depth below chart datum. Samples were taken on SCUBA by scraping each quadrat and collecting all material using an air-powered underwater vacuum. Percent cover of encrusting species was visually estimated in each

quadrat and species too large for the vacuum opening were measured, recorded and removed from the quadrat. One diver then proceeded to scrape the substratum to dislodge species for the second diver to vacuum into a nylon sample bag. Larger invertebrates were identified and weighed and returned to the field, while the remaining invertebrates in each sample were stored in 3% formalin for later sorting in the lab. Samples were transferred stepwise from 25% ethanol to 75% ethanol for storage and stained with Rose Bengal to highlight tissue for identification.

We converted kelp and invertebrate sizes and densities to biomass using length-weight relationships found in the literature. For species for which allometric relationships were not available, power equations were fit to approximately 30 individuals from each transect to determine the relationships between size and weight. This allowed total biomass to be calculated for each species. For mesograzers and sessile invertebrates processed in the lab, sorted samples were weighed to the closest tenth of a milligram to measure the biomass of each taxon or taxonomic grouping. Finally, we converted biomasses to densities (per m^2) and scaled them to the study area (Table S1).

These field data were supplemented with literature values for unsampled groups, production (P/B) and consumption (Q/B) rates (Table S1), and diet composition (Table S2). Data availability from the literature was variable, with commercially harvested species typically being better studied. Model parameters were derived from these diverse sources and entered into the model. The model was then balanced to ensure sufficient biomass across the trophic flows. It is notable that very little adjustment was necessary to achieve this balance (see Model balancing and tuning section below), indicating that a reasonable (or at least consistent) set of parameters was derived.

Ecosystem dynamics were parameterized using the field data according to space-for-time substitution. Sea otters were then introduced into the model and it was run to a new equilibrium

representing an otter-present state. Details on how parameters for each species or functional group were derived, and the parameterization of the temporal dynamics, are provided in the trophic model structure and parameterization section below.

3. Estimating model uncertainty

Despite being a desirable component of modelled results, uncertainty continues to be a largely ignored topic in ecosystem modelling (14). In this study, parametric uncertainty was examined in both the trophic model, and in the translation of system biomass to economic benefits.

The uncertainty in the trophic model was assessed by generating 1000 randomized, balanced Ecopath models and their corresponding otter-present states with Ecosim. Ecopath base parameters were re-sampled using a Monte Carlo simulation. The B , Q/B , and P/B of the balanced, otter-absent model were permuted using a uniform distribution centered on the balanced value, with a coefficient of variation proportional to the presumed accuracy (low, medium or high) of the parameter (Table S3). High quality was assigned to parameters derived from data collected in the study area, and for which the habitat proportion could be reliably scaled. Biomass was assigned a value of Medium where data quality was high, but habitat scaling was speculative, and Low where both data quality and habitat scaling were poorly known. For P/B and Q/B (which were primarily obtained from the literature) quality was assigned based on the author's familiarity with the functional groups, and the similarities between the literature and this study area. Diet parameters were all permuted using low accuracy (and a coefficient of variation = 0.8), to allow the maximum range of potential models to be explored. A Visual Basic routine was used to repeatedly generate permutations of otter-absent Ecopath models until a sample of 1000 balanced models was obtained.

It was difficult to tell, *a priori*, how effective the permutations would be at generating balanced models (i.e., it is reasonable to expect that excessive randomization of the base and diet parameters would have a very low probability of generating a balanced model). A conditional reduction in the coefficient of variation was therefore used to ensure the permutations led to balanced models. This reduction was a combination of a threshold on failed permutation attempts and a constriction applied to the standard deviation should the threshold be exceeded. The randomization was configured with a threshold of 100 attempts, and a constriction of 5% of the standard deviation each time the threshold was reached. To ensure the later scenarios were not overly constrained, no constrictions were applied once 10 balanced scenarios were obtained.

Randomized, balanced models were run through Ecosim to generate a corresponding 1000 alternate future scenarios. The predicted changes from these paired models represent the change in B of the ecosystem service providers from which the ecosystem services are calculated (Figure 2). The distribution of values from the 1000 alternate scenarios represent the uncertainty of trophic model parameters. For each ecosystem service, additional variability was added to represent the uncertain aspects of the service valuation, as described in the following section.

The final representation of uncertainty (Figure 3) is a product of the parametric uncertainties at each step in the process, from the estimation of changes in biomass through to the valuation of the services. The resulting cumulative uncertainty bounds are described as credibility estimates because they integrate the most significant model uncertainties, thereby providing an assessment of the how credible the overall models results are.

4. Valuation of ecosystem services

Four ecosystem services were estimated from the biomass of ecosystem providers predicted by the trophic model. These included existing fisheries, supplemented catch, carbon

sequestration, and tourism. For each service, uncertainties were included by drawing 1000 random values for key parameters and pairing them with the 1000 balanced trophic models.

4.1. Existing fisheries

This service is comprised of five established commercial fisheries (red sea urchin, Dungeness crab, geoduck clam, other edible clams, and lingcod), all represented in the modelled ecosystem. Catch data were obtained from Fisheries and Oceans Canada for the management areas within the study area for the years 1983 to 2008. The mean annual catch was used as the fishing mortality rate in the trophic model after converting to density (t/km/yr) based on the study area (Table S4).

The total catch by existing coastal fisheries for both otter-absent and otter-present states was calculated by multiplying the corresponding 1000 biomass estimates by a constant fishing mortality for both periods. This produced 1000 randomized catches, paired for otter absent and otter present models. Using a constant catch rate assumed the same proportion of available biomass was harvested in both states – a reasonable assumption from the perspective of fisheries management. This average was used instead of more detailed catch per unit effort estimate because effort data are not collected for all species. The long-term average also produced more conservative results, as it would maximize the predicted loss (because larger catches tend to occur earlier in a fishery).

The value of a catch can be highly variable, changing in response to a range of social and economic factors. To partially account for this variability, the landed values for both states were sampled from a distribution of landed values with a mean and standard deviation calculated from 10 years (2001-2010) of regional catch data (Table S4). The final values were differenced to estimate the change in the value of the catch. In the absence of a reasonable prediction of future

prices, it was assumed they would fall in the range of the historic prices. Uncertainty in this ecosystem service thus integrates the variability in the biomass predictions with price uncertainty. Landed values were converted to 2018 CA\$ using the Canadian consumer price index (54).

4.2. Supplemented catch

This part of the analysis assumed the portion of the biomass produced but not directly consumed by modeled groups was available for consumption within the broader ecosystem. This service is thus defined as a nutritional supplement to higher trophic level finfish. Annual model surplus is defined as the biomass produced but not consumed each year by the groups explicitly represented in the model.

Surplus production has three possible fates. It can enter the food web, wash up on beaches as wrack (organic material such as kelp and sea grass that is cast up onto the beach by surf, tides, and wind), or be transported to the deep ocean and be sequestered. Because the fate of kelp (and other surplus production) is poorly known, it was apportioned to the three different fates by first drawing a proportion for carbon sequestration from a uniform distribution on the range [0.1, 0.5] (the range of values explored by (29)). Given a lack of additional information, the remaining surplus biomass was then apportioned equally to wrack and the food web. The translation of the portion entering the food web (i.e., the nutritional supplement) into valued supplemental catch is described below; the estimation of the value of carbon sequestration is described in the following section. The value of beach wrack is not considered.

The predicted dollar value of this indirect ecosystem service was based on the amount of surplus biomass transferred to high value finfish species via trophic transfer (i.e., food web consumption), and an estimated landed value of these species based on historic data. Surplus

biomass was estimated for three trophic levels. Trophic level 3 included fish consumed by the high value species (forage fish, pelagic reef fish, other demersal reef fish), trophic level 2 included primary consumers such as grazers and zooplankton (kelp crab, predatory invertebrates, grazers, sessile invertebrates, and large zooplankton); and trophic level 1 included the kelp groups (giant kelp, bull kelp, and other kelps). The biomass transferred to the high-value finfish was calculated separately for each trophic level, with each level transferred the appropriate number of times to reach the high-value finfish:

$$\begin{aligned}
 \text{Supplement \$ Value} = & \sum_{i=1}^{N_{TL3}} (NPP_i * TTE1 * \frac{\$}{\text{tonne}}) + \\
 & \sum_{i=1}^{N_{TL2}} (NPP_i * TTE1 * TTE1 * \frac{\$}{\text{tonne}}) + \\
 & \sum_{i=1}^{N_{TL1}} (NPP_i * TTE1 * TTE1 * TTE2 * \frac{\$}{\text{tonne}})
 \end{aligned}$$

For each group (i) in each trophic level (TL3, TL2, TL1), the value of the surplus production was calculated by scaling the total net present production (NPP) for the group ($B * P/B$) by the proportion of B not accounted for in the model ($1-EE$). Thus for any functional group, assuming there are no unaccounted for mortalities, surplus $NPP = B * \frac{P}{B} * (1 - EE)$. This surplus was scaled to valued finfish species by estimating a trophic transfer efficiency for each trophic level. Two trophic transfer efficiencies were used. The first (TTE1) representing transfer between predators and prey, was randomly sampled from a normal distribution parameterized (mean = 0.1013, standard deviation = 0.0581) according to (55). The second (TTE2) recognizes that the trophic transfer efficiency from primary production to mesozooplankton is higher, and was therefore sampled from a distribution with the same standard deviation but a mean = 0.25 (Wade 2000 cited in (56)). Random samples from both trophic transfer efficiencies were truncated at

zero. The resulting nutritional supplement was multiplied by a value drawn from a triangular distribution bounded by a 10-year average annual landed value (2001 to 2010) of the least and most expensive commercial finfish (i.e., rockfish at 1.91 CA\$/kg and halibut at 9.38 CA\$/kg) (data S1), with a mode of 2.99 CA\$/kg – the weighted average of the adjusted 10 years of annual landed value of all commercial finfish (i.e., halibut, lingcod, rockfish, and salmon). Landed values are reported in 2018 CA\$ after converting with the Canadian consumer price index (54).

Uncertainties considered in this service include the total surplus production (from the trophic model), the bioavailable portion of surplus production, the efficiencies of the trophic transfer pathways, and the landed value of the supplemented catch when sea otters reach carrying capacity. While this does not represent all the uncertainties arising from the vagaries of the social-ecological system (such as species interactions and market forces across a range of space and time scales), many of these simply cannot be estimated with any degree of certainty. However, by including a range of uncertainties from across the production chain, this analysis provides a credible, and likely conservative, indication of the range of potential values.

4.3. Carbon sequestration

The annual dollar value of carbon sequestration was obtained by estimating the proportion of the surplus kelp production lost to deep flux, and multiplying it by the average price:

$$\text{Annual \$ Value} = kNPP * \%D * \%C * \text{Deep Flux} * \frac{\text{mm } CO_2}{\text{mm C}} * \frac{\$}{\text{tonne } CO_2}$$

Total kelp net primary production ($kNPP = B * P/B$) was estimated by combining B and P/B for the three kelp groups by summing B and calculating a weighted average of the P/B ratios. The resulting $kNPP$, in wet tonnes/km²/year, was converted to total carbon using percent carbon

(%C=26.6, SD=2.8) and percent dry (%D=17.3, SD=1.92) values from (29), measured for giant kelp. It was assumed that %Dry = 1 - %Wet, the reported value.

To estimate the value of carbon (\$/tonne C) given historic fluctuations and projections of significantly higher future costs, we sampled this parameter from a triangular distribution with a minimum value based on average European Union price of CO₂ from 2012 to 2017 (EU27.23), a median value based on the peak 2018 price (EU67.06), and a maximum based on an industry forecast of EU238.27 per tonne of CO₂ by 2030 (57). In addition, because the EU price is for CO₂, the proportionally higher price for a tonne of C was calculated based on the respective molar masses (mm). Each random value was converted to CA\$ using an exchange rate re-sampled from a normal distribution parameterized with a mean (1.46) and standard deviation (0.091) based on historic exchange rates from 2000 to 2018. Given the many uncertainties associated with C pricing, the resulting value was assumed to be equivalent to 2018 CA\$.

This valuation yielded a value about one third that of (29), using the same dollar value. This corresponds to a similar difference in the net primary productivity used in the two studies, and is due to a significant difference in the respective estimates of standing stock in otter-present areas. The estimate of 9 to 16 kg kelp per m² from (29) in otter-present systems is five to ten times higher than the densities used in this study. The lower densities used in this study are a function of using the trophic model to estimate biomass based on assumed ecotrophic efficiencies. This is standard practice for estimating biomass in trophic models (53), and provided a parsimonious solution to the challenge of estimating biomass for species' whose standing stock changes by orders of magnitude both seasonally (through growth) and inter-annually (through loss to storms). A consequence of this design decision is that the value of both the carbon sequestration and supplemented catch services are conservative, and may be considered a lower bound on

these values. See the discussion on variability in measures of kelp biomass (below) for more details.

In addition to the uncertainties estimated for total surplus production (from the trophic model), the final predicted value of carbon sequestration included uncertainties relating to the fate of kelp, its dry weight and carbon content, and the price of carbon.

4.4. Tourism

The estimate of increased tourism revenue due to sea otters was based on a choice experiment and survey of Vancouver Island visitors (30). The experiment revealed that willingness-to-pay for a nature tour increased by an average of CA\$121 per visitor if the trip had a very high vs. a low chance of seeing sea otters. For comparison, the marginal increase in willingness-to-pay for a high chance of seeing a whale was \$195 indicating the high value of these specialized wildlife tours. The experiment also found that the number of visitors taking a wildlife tour would increase by 7.4% if sea otter sightings could be guaranteed. The contribution of sea otters to tourism revenue was therefore estimated by multiplying a predicted number of visitors, by the increased proportion taking a wildlife tour, and by the increased willingness-to-pay for a wildlife tour.

The number of tourists was sampled from a normal distribution with a mean (776,310) and standard deviation (22,170) calculated from 5 years of available visitation data (2009-2013) for the regional national park (data S2). The proportion taking a wildlife tour was sampled from a uniform distribution with a range of [0.35, 0.54]. This range was obtained by adding 7.4% to a minimum tour rate reported by the park (27.6%) and the maximum value reported for the region (47%) (30). Finally, the marginal increase in the value (CA\$) of a wildlife tour was sampled from a normal distribution with a mean (120.7) and a standard deviation (36.7) taken from (30).

The uncertainties considered in this service include number of visitors, their likelihood of taking a wildlife tour, and the marginal increase in the cost of taking such a tour. Given the high uncertainty associated with estimating the increased value of tourism, the resulting value was assumed to be equivalent to 2018 CA\$.

While the predicted increase in tourism revenue is significant, there are a variety of other ways this could be calculated from the available data. For example an estimate of CA\$14.9M to CA\$15.2M is reported by (30), but this is intentionally conservative, using only the increase in number of visitors taking a wildlife tour. Alternatively, an upper estimate would incorporate the willingness-to-pay value, and assume that all wildlife tourists would pay the increased marginal cost. Using the higher regional visitation numbers used by (30) instead of the more conservative park visitation rate used here yields a point estimate of CA\$69.4M. These upper and lower estimates fall just outside the 95% credibility estimate reported, adding additional credibility to the results.

We emphasize that this value estimate is a potential benefit, the realization of which will depend on local values and infrastructure (i.e., the ability to attract tourists). We also note that the realization of any such potential value will depend on a range of social factors and vary spatially. Further, although this analysis is based on a local study, coastal British Columbia shares many characteristics with southeast Alaska, where tourism is also a burgeoning industry (31), and access is often constrained to water access only. Some parts of southeast Alaska are more established in this regard compared to our study area as cruise ships regularly visit more remote communities, providing guests with wildlife experiences similar to those assessed in our work (e.g., 58). Additionally, should sea otters expand to more populous regions such as the Salish Sea the potential benefits of tourism may well be higher than we predict.

5. Trophic model structure and parameterization

The study area encompassed all sea otter foraging habitat on the West Coast Vancouver Island, British Columbia, Canada (Figure 1). It included 4112 km² of hard and soft bottom marine habitats to 50 m depth, the practical limit for sea otter foraging (27).

Sea otters are effective at limiting populations of benthic invertebrates, most notably sea urchins, clams, abalone, large crabs, and mussels (59). When abundant, sea urchins are consumed preferentially, likely because of ease of capture. As urchin abundance is reduced, sea otter diet diversifies to other prey (60, 61). In areas with soft sediment, sea otters often excavate bivalve prey including butter clams, horse clams and geoduck clams (62).

In the eastern North Pacific, the preferential consumption of sea urchins as sea otters re-occupy former habitats releases kelp from grazing pressure and can trigger a trophic cascade leading to a kelp-dominated ecosystem (8, 9). Representing this dynamic was an explicit objective of the trophic model configuration.

The model was parameterized with field data on the abundance of key species collected in areas where sea otters are absent, and where they are at carrying capacity (Table S1). Published parameters were used for groups not sampled. Diet proportions in trophic models can be based on observations where available. For example, identification of sea otter prey is based on observational diet studies that document prey brought to the surface and consumed by sea otters. Other studies have identified diets (primarily of fishes) by examining gut contents. When direct observations are unavailable, aggregated sources (e.g.,63) or other models can be consulted, or generalizations from other species or groups can be made. Ecosystem models representing a particular dynamic, such as the trophic cascade modelled here, appear relative robust to uncertainty in diet composition (64).

Abundance of key species needed to be scaled to the study area because Ecopath uses average biomass across the area of interest. Since abundance data are typically collected where a species is known to occur (i.e., in suitable habitat), an understanding of the proportion of the suitable habitat within the entire study area is required to correctly scale the density data. This is a critical challenge facing the translation of local field data to management-relevant models.

A key part of translating local field studies to regional models involves scaling the observations to the study area. Several assumptions were required to scale the data in this study. First, following (65), it was estimated that 30% of the study area is rocky reef. It was also assumed that 30% of the total study area was suitable for infaunal organisms (i.e., soft-bottom), and that depths were uniformly distributed between 0 and 50 m. How these assumptions are applied to scale the individual groups is described below. The uncertainties in these structural assumptions were not directly assessed, but were developed to be conservative estimates of habitat extents.

5.1. Trophic parameters

Parameters were derived for biomass (B), production (P/B), and consumption (Q/B) for the groups in the model (Table S1) based on species-specific, empirical data collected within the study area where possible. For functional groups, or less studied species, values from earlier models of the study area were considered. In particular, a recent analysis of an ecosystem with many of the same species and groups (66) was broadly consulted, as well as earlier models for the same region by (67-69). All estimates derived from these models were applied to the otter-absent system, as that is the period for which the models were developed.

For poorly understood species, the P/B ratio was estimated using allometric scaling following (70) and (71) using individual weights and various life history characteristics.

Occasionally, species lengths were first converted to mass following (72). Details on the application of this approach can be found in (73). Similarly, B data are typically unavailable for non-commercial species, and may not even exist for valued species. In these cases, standard practice is to estimate B using an assumed ecotrophic efficiency (EE). See (53) for details.

Sea otters

Population and diet parameters for sea otters are among the most reliable, the species having been extensively studied. Information from otter-present and otter-absent areas was used to parameterize the Ecosim transition from an otter-absent to otter-present state.

Biomass: In the otter-absent model, $B = 1 \times 10^{-6} \text{ g/m}^2$ was used as a placeholder for the subsequent reintroduction biomass. To then seed the population recovery trajectory and generate the otter-present state, $B = 4.33 \times 10^{-4} \text{ g/m}^2$ was calculated as the biomass of introduced sea otters (based on 89 animals with mean weight of 20 kg (74) in a study area of 4112 km²). Similarly, a carrying capacity of $B = 0.040$ was estimated for the study area based on 8,303 animals (73).

Production: The initial population growth rate ($P/B = 0.186$) was taken from (75).

Consumption: Sea otter Q/B was estimated using the midpoint (28%) of the daily ration (23-33% of body weight) reported by (59). This gave an initial annual consumption rate of $0.28 \times 365 = 102.2$. However, upon model validation, this value was raised to $Q/B = 140.0$ to keep the carrying capacity in line with the sea otter population model. It is not an unreasonable increase given the unrestricted food supply during the sea otter expansion (see (73) for details).

Diet: Sea otter diet composition (Table S2) was based largely on (76) who described a diverse diet in areas where otters were established, and a more limited diet in a newly occupied

area. In the newly occupied area they found the sea otter diet dominated (70%) by sea urchins (*Mesocentrotus* and *Strongylocentrotus* spp.) with the balance (~25%) comprised mainly of large bivalves. In contrast, the diet where otters were established was dominated by bivalves (~50%) and predation on urchins was negligible. Other components of the diet included large crabs (~5%), other crustaceans (~5%), predatory invertebrates (i.e., *Tegula* spp., octopus) (10%), with the balance split between large grazers (i.e., chiton) and sessile invertebrates. A diet dominated by sea urchins and bivalves was therefore assigned in the model, although the diversity of prey species known to have occurred in the study area (e.g., abalone, Dungeness crab, geoduck clams) was included to allow the model to adjust diet based on changing prey abundance.

Sea urchins

This group includes red (*Mesocentrotus franciscanus*), purple (*Strongylocentrotus purpuratus*), and green (*S. droebachiensis*) sea urchins. Red sea urchins are the largest of the five urchin species found in the eastern North Pacific. They inhabit rocky substrate mainly from the intertidal zone to 50 m, though individuals can be found to 125 m (77). The smaller green and purple urchins have similar ranges and diets, but in British Columbia are less important commercially.

Biomass: Previous models of the study area have used biomass values ranging from 6.7 to 30 g/m². Average densities (1.11 and 2.011 /m²) and biomass (455.29 and 669.92 g/m²) of harvestable red sea urchins (> 90 mm) were reported by (78) for two otter-absent areas in the study area. The mean of these values gives $B = 562 \text{ g/m}^2$, which is well less than the potential maximum densities (2.67 urchins/m²) and biomasses (1204.07 g/m²) recorded as part of this study and in other nearshore systems. For example in the western North Atlantic, B in urchin barrens is reported as 1100 - 1200 g/m² (79).

Even higher values of urchin B (ranging from 2800 to 3400 g/m²) have been observed from rocky reefs in an adjacent otter-absent area (9). The same study shows pre-otter B in the area of sea otter introduction declining from a maximum of 2900 g/m² to as low as 25 g/m² 30 years post-introduction (9). Thus, while there is a potential for very high sea urchin densities, there is also considerable variability. The differences in observed B could be due to a range of factors including regional, temporal, or sampling differences. For consistency, the pre- and post-sea otter biomasses of sea urchins from the reintroduction area were used to represent the change in B between otter-absent and otter-present areas. Since sea urchins are found almost exclusively on rocky reefs, B was scaled using the 30% rocky reef assumption, and an additional assumption that only 30% of rocky reefs were suitable oceanographically. The resulting 10% habitat suitability assumption (rounded up from 9%) scaled the field observations to initial estimates of $B = 290$ g/m² for the study area in the otter-absent state, and $B = 2.5$ g/m² in the otter-present state (Table S1). However, the model did not reproduce the trophic cascade when sea otter prey were abundant. The sea urchin biomass was therefore further reduced in the sea otter-absent state to $B = 29$ g/m². This decision was supported by evidence that sea urchins exhibit reduced reproductive rates at high densities (80). See (73) for more details.

Production: Sea urchin reproduction is poorly understood, and recruitment events happen infrequently when populations are high (81). Sea urchin P/B was therefore estimated using the Brey method based on the mean test size (79.2 mm) of pre-sea otter sea urchins reported by (9) giving a mass of 186 g and a $P/B = 0.244$. This value is likely an under-estimate as it does not consider the higher P/B of the shorter-lived green urchin (66).

Consumption: Sea urchin consumption was reported as $Q/B = 10.9 \text{ yr}^{-1}$ by (66) based on laboratory tests (82). This value was adopted recognizing that a lower value may be more appropriate in a nutrient-limited environment such as an urchin barrens.

Diet: In an urchin barrens adult red sea urchin diet is comprised almost exclusively of fleshy algae, while juveniles tend to forage on detritus, coralline algae and other surface scrapings (83). Green urchins are known to actively climb and feed on live kelp (66). A diet similar to (66) was therefore used, but with the proportion of kelp detritus increased to account for its greater abundance in the study area, and observations that in kelp forests, sea urchins are less active grazers, preferring to passively wait for kelp detritus (84). Urchins are preyed on by sea otters, Dungeness crab, kelp crabs, and other predatory invertebrates.

Dungeness crab

Dungeness crab (*Metacarcinus magister*) is the second most valuable invertebrate in Pacific Canada (data S1) and is by far the dominant large crab species in the region. The fishery is seen as fully exploited, and catch has been relatively stable indicating reasonably successful management. The species is also very important for recreational fishing. Two other crab species (Pacific rock - *Cancer antennarius*, and red rock – *Cancer productus*) are caught commercially, however catches of these less valued species are small compared to Dungeness. Parameters for this group are derived primarily from the Dungeness crab literature. However some attention is paid in the diet to include the other species which are considered to be more predatory.

Biomass: Stock assessments provide an average weight of Dungeness crab caught (740 g/crab; (85)), but no published abundance estimates for Pacific Canada were found, likely because the fishery is conservatively and effectively managed using size and sex restrictions (85). The only density data found was from a multi-year study in the Columbia River estuary

(86). These data illustrate the high inter- and intra-annual variability in crab densities, making such direct measures difficult. Therefore, following (66), Ecopath was allowed to estimate B using a presumed $EE = 0.90$.

Production: A $P/B = 1.50$ was assigned based on the average from two earlier models of the study area (67, 69). This corresponded well with the value estimated by (66).

Consumption: Similarly, a $Q/B = 4.25$ was assigned based on (69) and (67). This corresponded well with the value estimated by (66).

Diet: Crabs are often viewed as opportunistic predators, with the diet described as containing a variety of crustaceans, bivalves, polychaetes, juvenile fish, and algae (87). However, such studies are based on stomach contents, and often conducted in estuaries. It is therefore not clear whether this diet diversity is due to active predation, or the scavenging of dead individuals (i.e., detritus), which may be more common in estuaries. While it is reasonable to envision Dungeness crabs preying on sessile invertebrates, it is harder to imagine them capturing mobile fish species. Thus, reports of juvenile fish in the diet, and perhaps other species, from studies based on stomach contents, are more likely a result of scavenging rather than direct predation. The implication that Dungeness crab prey on forage fish (66, 87) does stretch the imagination. Thus, in keeping with the idea of Dungeness crabs as primarily scavengers, a diet dominated by sessile invertebrates (0.34), followed by detritus (0.25) and other edible clams (0.10), with equal (0.05) proportions to sea urchins, mussels, kelp crabs, predatory invertebrates, large grazers, small grazers, and 0.01 cannibalism was assigned (Table S2).

Edible bivalves

To capture the commercial provisioning services of these species, they were divided into three groups: geoduck clams, mussels, and other edible clams. Japanese oysters (*Crassostrea gigas*) were excluded from the model because it is not a known prey item of sea otters in British Columbia.

Diet: The diet of these three groups was assumed to be similar, comprised largely of particulate organic matter. However, since particulate organic matter was not explicitly represented in the model, assumptions about the proportions from potential sources (which can include early life history stages of some species) were needed. In an otter-absent state, it was assumed that most of the particulate organic matter was derived from phytoplankton (0.78) with contributions from both kelp detritus (0.10) and detritus (0.10), and a possibility (0.01) each from the large zooplankton and small heterotrophs groups (Table S2). Biomass, production, and consumption are described for each group below.

Geoduck clam

Geoduck clams (*Panopea generosa*) are the most valuable commercial invertebrate fishery in Pacific Canada (data S1). Geoduck clams are found from the intertidal to depths of 100 m (88), however dive harvesting occurs in depths less than 20 m. Besides humans and sea otters, adult geoduck clams have no known natural predators. Predation mortality during larval and early-burrowing stages is presumed to be similar to other species with a larval and settlement life history.

Biomass: Species-specific parameters from stock assessments (77) were used to estimate *B*. Mean geoduck clam weight in the study area is reported as 1.0 kg, with wild densities ranging

between 0.54 and 0.86 per m². This suggests a B between 540 and 860 g/m² in suitable habitat. This is considerably lower than the observed bed density of 1590 g/m² in Southeast Alaska (89), suggesting geoduck clam densities and perhaps habitat suitability are highly variable. The midpoint of the British Columbia estimate was scaled to the study area by applying the 30% soft bottom assumption and an additional 30% oceanographic suitability assumption yielding a 10% habitat suitability, which scaled the 700 g/m² midpoint to $B = 70$ g/m². This is slightly more than the estimate of 52.4 g/m² from (66), which they describe as conservative.

There is some uncertainty around the impacts of sea otters on geoduck clams. Anecdotal reports from fishers suggest the reduction of geoduck clam density in otter-present areas is significant. However, this does not always seem to be borne out by the data. One study (90) found no difference in geoduck clam density between groups of sites with and without sea otters, although this appears to have been confounded by significant inter-annual variability. In Southeast Alaska, the ratio of mean geoduck clam B between surveyed beds with and without otters is 0.87, although a reduction in the size distribution is evident (89). A factor of 0.80 was therefore used to estimate $B = 56$ g/m² in otter-present areas (Table S1).

Production: Following (66), the estimated exploitation rate of 1.2% (77) was added to the mean (0.036 yr⁻¹) of a natural mortality estimate of between 0.014 and 0.054 yr⁻¹ (90) yielding a $P/B = 0.048$ yr⁻¹. This is in line with the 0.036 yr⁻¹ used by (66), but considerably less than the 0.125 yr⁻¹ estimated with allometric scaling (73) suggesting the value could be low.

Consumption: A $Q/B = 2.0$ yr⁻¹ was adopted from (66).

Mussels

Mussels (*Mytilus californianus*) occur attached to hard substrate in highly exposed areas of the coast. This is in contrast to *Mytilus edulis* described in (66) or *M. trossulus* (more commonly found in British Columbia) which prefer relatively protected estuarine bays. Mussels feed a range of groups including predatory invertebrates, Dungeness crab, pelagic reef fish, and other demersal reef fish.

Biomass: Local work estimated a remarkable $B = 82,600 \text{ g/m}^2$ in suitable habitat from field surveys (91). In otter-present areas, they found these values to be somewhat lower ($B = 57,100 \text{ g/m}^2$).

To scale this sizable biomass to the study area, and bring it more in line with the other bivalve groups, it was conservatively assumed that suitable mussel habitat, because of their exposure requirements, comprised only 1% of the 10% of the study area assumed to be shallow rocky reefs. This scaling factor (0.001) gave a still substantial $B = 82.6 \text{ g/m}^2$ for otter-absent areas. Without assessments of mussel habitat suitability, the reasonableness of this assumption is difficult to assess. However, the value is in line with the other groups in the model.

Production: A $P/B = 0.428 \text{ yr}^{-1}$ was obtained using allometric scaling to first estimate the energy per individual, and then P/B from energy and life history characteristics.

Consumption: Following (66), $Q/B = 1.42 \text{ yr}^{-1}$ was estimated by dividing the P/B estimate (above) by a presumed bivalve growth efficiency of 0.3 (see (73) for more details).

Other edible clams

Five commercial species of clams are found in the study area including Manila (*Venerupis philippinarum*), littleneck (*Protothaca staminea*), butter (*Saxidomus giganteus*), razor (*Siliqua*

patula), and varnish (*Nuttallia obscurata*) clams. For the purposes of this analysis, the group was restricted to the 3 most valuable species: Manila, littleneck and butter clams.

Butter clams dominated landings prior to 1980, after which the majority of landings were Manila clams (92). Butter clams are also an important prey item for sea otters in southeast Alaska (62).

Biomass: A method for estimating B was derived using species-specific parameters from stock assessments, and other related references (73). The method first assumed that harvest reference points described suitable habitat densities. The regional integrated fisheries management plan (92) describes a harvestable reference point of 30 legal size clams/m², although densities can be in excess of 130 legals/m². Legal sizes are: littlenecks (38 mm), butter (63 mm), manila (68 mm) and razor (90 mm).

Legal lengths were converted to weight. Razor clams were dropped at this stage because they are less widely distributed than the other species, contributing less to the B , and because growth information was not available. The weights for the remaining three species were converted to densities using the harvestable density reference points and summed the species minimum legal densities (30/m²) to generate a conservative estimate of total $B = 6,462 \text{ g/m}^2$ in suitable habitat areas.

To scale this B for the study area, the 30% soft bottom assumption was augmented by assuming only 30% had suitable water chemistry, and that the species' extended over only 10% of kelp suitable depth (based on the uniform depth assumption and a distribution to 5 m depth). The resulting realized habitat extent of (0.3*0.3*0.1) resulted in a potentially conservative $B = 58.2 \text{ g/m}^2$ for the study area.

Production: A $P/B = 2.059 \text{ yr}^{-1}$ for infaunal bivalves was estimated by (66), however their group also included the very small species which were excluded from this model. Thus, this number is likely high. For comparison, allometric scaling using the available data for butter clams yielded a $P/B = 0.410 \text{ yr}^{-1}$. This value was used, recognizing that it could be an underestimate.

Consumption: As with mussels, the $Q/B = 1.37 \text{ yr}^{-1}$ estimate was obtained using a typical conversion efficiency (P/Q) for bivalves of 0.3, allowing Q/B to be estimated from P/B (66).

Lingcod

A highly-prized greenling species, *Ophiodon elongatus* adults are found near rocks, ranging from the intertidal to 475 m depth. Young occur on sand or mud bottom of bays and inshore areas.

Biomass: The average biomass ($B = 0.33$) from three models (67-69) was used, assuming that lingcod were uniformly distributed across the region. These values were implicitly for otter-absent areas as the models were derived for otter-absent systems.

Production: Recent work on lingcod populations for three offshore lingcod areas in British Columbia (93) led to an average reproductive rate of 0.252. However, given that lingcod continue to be exploited by recreational fisheries, this was reflected in the $P/B = 0.50$ used, which is in the range between unexploited and exploited values discussed by (66).

Consumption: The average ($Q/B = 3.55$) of the values from the earlier models (67-69) was used.

Diet: Since lingcod forage extensively in deeper habitats not included in the study area, it was assumed that lingcod import 50% of their diet. The remaining 50% was divided into

proportions similar to those published elsewhere (94, 95): other demersal reef fish (0.15), pelagic reef fish (0.05), forage fish (0.05), kelp crabs (0.1), large grazers (0.07), small grazers (0.07), and lingcod (0.01) (Table S2).

Other demersal reef fish

The eastern North Pacific has the world's greatest diversity of rockfish (*Sebastes* spp.) with over 65 different species (96). These species are generally associated with rocky reefs. While demersal fish species tend to get larger in deeper waters where most spend their adult lives, the nearshore is home to younger conspecifics, as well as to adults of some smaller species. The deeper regions of the nearshore are part of the habitat of some larger rockfish, most notably lingcod. Of the remaining species, the most dominant in this group are other greenlings (Family Hexagrammidae) and black rockfish (*Sebastes melanops*). The group also includes sculpins and other larger species such as cabezon (*Scorpaenichthys marmoratus*) and red Irish lord (*Hemilepidotus hemilepidotus*).

The average values from the other large rockfish groups defined by (67, 69) gave $P/B = 0.14$ and $Q/B = 3.0$. However, since these values yielded a low P/Q ratio, values of $P/B = 0.24$ from (66), and $Q/B = 1.2$, calculated using an assumed $P/Q = 0.2$ (a standard value for fish (66)), were used. Model tuning raised these values to $P/B = 0.3$ and $Q/B = 2.0$ to make the respiration rate more realistic for these species. Ecopath was used to estimate B using $EE = 0.9$.

Diet: The diet of rockfish is highly diverse and consists largely of zooplankton (euphausiids, mysids, fish eggs/larvae), zoobenthos (e.g., amphipods, crabs, shrimp), and finfish (e.g., herring, sandlance, and rockfish). Reported ranges for several different species contained in FishBase (63) include: finfish 13-90%; zoobenthos 5-70%; and zooplankton 3-20%. To ensure the diet was broadly based, it was structured to include: sessile invertebrates (0.3), equal parts

meso-grazers and large zooplankton (0.2), equal parts (0.05) pelagic reef fish, kelp crab, small heterotrophs, some forage fish (0.02), and a possibility (0.01) of predatory invertebrates, large grazers, and small grazers, with a notable (0.10) cannibalism component.

Pelagic reef fish

This group includes species that spend the majority of their life history in the water column, associated with either the kelp forests on rocky substrates. It includes species such as the surf perches (Family Embiotocidae), and the tubesnout (*Aulorhynchus flavidus*), and bay pipefish (*Sygnathus grisolineatus*). Surf perches were explicitly represented by (97), while (66) defined a somewhat broader group termed demersal fish, that combined demersal species with these more pelagic ones.

A $P/B = 2.0$, and $Q/B = 10.0$ were used for this group. These values, slightly higher than those used by (66), were chosen to account for the shorter-lived characteristics of the group as defined, and to maintain P/Q near 0.20. Ecopath was used to estimate B using $EE = 0.8$, a value used by (66) for their demersal fish group.

Diet: Based on the data reported for a number of northeast Pacific species (63), the prey of this group includes small forage fish, and both planktonic and benthic crustaceans. These are represented in the model as large zooplankton and meso-grazer groups. The diet was therefore defined as largely large zooplankton (0.52) and meso-grazers (0.20), with equal (0.05) contributions from predatory invertebrates, large grazers, small grazers, small heterotrophs, and sessile invertebrates. The diet also allowed for the possibility of early life history forage fish, other demersal reef fish, and pelagic reef fish (0.01 each). The group forms a significant component of the diet of the larger fish groups.

Forage fish

This group includes the small, seasonally abundant, schooling species. They are differentiated from pelagic reef fish because their seasonal aggregations are important to many macro-organisms. In the eastern North Pacific this group includes primarily herring (*Clupea pallasii pallasii*), sand lance (*Ammodytes hexapterus*), anchovy (*Engraulis mordax*) and sardines (*Sardinops sagax*). All species were included as a single functional group since their ecological role and diets are similar (see (63)). The composition of this group differs from that typically defined for forage fish by more offshore, fisheries focused models which include more oceanic species such as smelt and mackerel, while often treating herring separately.

Assuming this group is dominated by herring, the average $Q/B = 4.75$ from (67-69) was used. While the Q/B corresponded well to the forage fish group of (66), the P/B average of 0.67 from these models seemed low. A $P/B = 1.5$ based on an integrated forage fish value (66) was therefore chosen. Ecopath was allowed to estimate B based on an $EE = 0.90$ given the role of forage fish in the ecosystem.

Diet: Examining the diet from earlier models shows that juvenile forage fish feed mainly on small crustaceans (both planktonic and benthic), also taking invertebrate larvae. Adults prey mainly on small crustaceans and fishes, and detritus. In this model these prey are represented primarily by large zooplankton (0.8) and meso-grazers (0.18) with the possibility of small grazers and sessile invertebrates (0.01). They are prey for many fish species (e.g., lingcod, other demersal reef fish, and pelagic reef fish), but usually only when aggregated.

Kelp crabs

While serving a similar ecological role as small grazers, the local kelp crab *Pugettia producta* also prey on sessile invertebrates and mussels, and likely some detritus. Along with decorator crabs and other small kelp-associated species, these animals contribute to the sea otter diet, thereby warranting their own group.

Biomass: Ecopath was allowed to estimate B for this group with an $EE = 0.90$. This assumed they play an important role as prey in the ecosystem.

Production: A $P/B = 3.5$ from (67) was used for this group, which corresponded well with the value (3.41) estimated by (66) for small crustaceans.

Consumption: Q/B for this group was estimated at 14.0 by (67), while (66) used $Q/B = 25$ for small crustaceans. A $Q/B = 20.0$ was chosen here.

Diet: Kelp crabs are more herbivorous than their larger counterparts (98) so they were assigned a significant (0.30) other macroalgae component. Mussels and sessile invertebrates are also key components of the diet (0.2 each). Detritus and kelp detritus were assigned equal proportions (0.10), and the rest was divided among small grazers (0.06) while also allowing for predation (0.01 each) on the other small, kelp associated groups including: sea urchins, predatory invertebrates, large grazers, and meso-grazers.

Other benthic invertebrates

The sheer diversity of smaller marine benthic invertebrates makes creating functional groups for these species a challenge in any trophic model. The first step was to exclude small, infaunal invertebrates (e.g., polychaetes, small bivalves, and other "junk in the muck") from the model because the focus here is on rocky reefs, sea otter prey, and commercial species.

Similarly, squid and jelly fish were excluded as they were considered primarily oceanic or not part of the sea otter diet. The remaining species were split into predatory invertebrates, epibenthic large grazers, small grazers, meso-grazers, and sessile invertebrates. These groups are intended to comprehensively cover nearshore invertebrate species that occur on rocky reefs, while allowing representation of size-based trophic associations.

The smallest (< 20 mm) pelagic crustaceans such as copepods and euphausiids were placed in the large zooplankton group.

Biomass: Biomasses for all groups were based on the data collected during dive surveys of rocky reefs to support this study. All observed biomasses were scaled using the 10% kelp habitat assumption. On balancing the model, it was necessary to increase the biomass of the small grazers group from 1.0 to 2.0, and during model evaluation, the B values for the otter-present region were reduced by an additional 50% to maximize model fit to the time series.

P/B and Q/B values were considered separately for each group.

Predatory invertebrates

This group includes the larger, predatory invertebrates such as the large sea stars, predatory snails (e.g., the moon snail), as well as whelks and oyster drills.

Production: A $P/B = 0.52$ for sea stars and 1.01 for predatory gastropods was estimated by (66). The mean of these two values was chosen giving $P/B = 0.76$.

Consumption: A $Q/B = 2.6$ for sea stars and 6.73 for predatory gastropods was estimated by (66). A value of $Q/B = 4.0$, slightly lower than the mean because sea stars dominate the relative abundance in this group, was chosen.

Diet: Predatory invertebrates feed on a diversity of other benthic invertebrates. Large sea stars feed primarily on mussels, barnacles (sessile invertebrates), small urchins, and limpets and snails (small grazers) while moon snails feed primarily on members of the other edible clams group (99). Since it is likely that other benthic invertebrates are also consumed by this group, a broad diet was designed, with equal (0.2) proportions to mussels, other edible clams, small grazers, and sessile invertebrates, 0.10 to detritus, and the remainder divided equally (0.02) among sea urchins, kelp crabs, predatory invertebrates, large grazers, and meso-grazers.

This group is preyed upon by sea otters, Dungeness crabs, lingcod, other demersal reef fish, and predatory invertebrates.

Large grazers

This group includes benthic invertebrates that serve as a significant food source for sea otters such as the large active grazers (i.e., abalone, turban snails, large chitons) as well as the more passive large sea cucumbers. Sea urchins, while certainly a large grazer, are in their own group because of their commercial value.

Production: A $P/B = 0.75$ for a different grazers group that includes chitons and small gastropods was estimated by (66), while (100) estimated abalone mortality in the absence of sea otters at 0.25. As the large grazer group used here included both these subgroups, a $P/B = 0.40$ was used, a value somewhat less than the mean of these values.

Consumption: (66) estimated a $Q/B = 8.9$ for the other grazers group and 11.3 for the large sea cucumber group. The mean of these two values ($Q/B = 10.1$) was chosen.

Diet: This group is herbivorous and thus feeds largely on kelp detritus (0.68) and the other macroalgae (0.20) groups. The inclusion of large sea cucumbers adds a significant detritus (0.10)

portion to the diet. The possibility of active grazing on either canopy kelp was allowed (0.01). This group comprises a significant portion of a diversified sea otter diet, as well as contributing to the diet of Dungeness crabs, pelagic reef fish, other demersal reef fish, kelp crabs, and predatory invertebrates.

Small grazers

This group includes active grazers too small to serve as sea otter prey (i.e., small snails and shrimp, limpets, periwinkles, small chitons). Since it falls functionally between the large and meso-grazers, values in between these groups were used: $P/B = 3$ and $Q/B = 14$.

Diet: Feeding primarily on large pieces of kelp detritus (0.88), this group is responsible for breaking down larger pieces of algae into smaller ones. A portion (0.10) of the diet was assigned to other macroalgae to accommodate direct grazing on encrusting algae and other benthic species, and the possibility (0.01) of direct grazing on canopy kelps was also allowed. Small grazers are preyed upon by Dungeness crabs, other demersal reef fish, pelagic reef fish, forage fish, kelp crabs, and predatory invertebrates.

Meso-grazers

This group is comprised of grazing benthic invertebrates too small to be sea otter prey, and includes a wide variety of small crustaceans such as brachyuran crabs, amphipods, mysids, and isopods. The group is equivalent to the small crustaceans group defined by (66), who describe it as among the most important groups in the system in terms of its structure and flow.

Production: Natural mortalities for amphipods in the literature range from 1.5 to 4.5 while for mysids it can be as high as 6.0. These values correspond well to the $P/B = 3.41$ used by (66) and that value is used here.

Consumption: A $Q/B = 25$ was used in earlier models (66). However, here that value led to excessive respiration rates so the rate was lowered to $Q/B = 15$ for this group.

Diet: Amphipods are mainly detritivores and scavengers, while mysids eat primarily algae and detritus in addition to some infaunal benthic invertebrates and zooplankton (101, 102). However, the small crabs in this group are more predatory, potentially taking mussels and other edible clams, as well as young stages of predatory invertebrates, and other meso-grazers. Since the grazers in this group continue the decomposition of detritus and algae into particulate organic matter suitable for filter feeders, half their diet was assigned to detritus, with equal proportions (0.10) to phytoplankton, kelp detritus, other macroalgae, and cannibalism. The remaining 0.10 was divided between small heterotrophs (0.08), and mussels and other edible clams (0.01 each).

This group can dominate the diet of larger animal groups such as predatory invertebrates, juvenile pelagic reef fish, forage fish, and other demersal reef fish.

Sessile invertebrates

This diverse group includes filter feeders (i.e., barnacles, tube worms, sponges, anemones, and small sea cucumbers and bivalves) too small to serve as sea otter prey. It includes species from the suspension feeder, deposit feeder, tunicate, and barnacle groups defined by (66).

Production: Considering what might be the relative abundances of these groups in the study area, an arbitrary $P/B = 2$ was chosen. This is in the range of all the similar groups used by (66).

Consumption: Considering the relative abundances of these groups in the study area, an arbitrary $Q/B = 13$ was chosen. This is in the range of all the similar groups used by (66).

Diet: The group has a diverse diet, consuming anything of an appropriate size including both zooplankton and phytoplankton. A balanced, diverse diet was assigned including large zooplankton (0.30), small heterotrophs (0.30), phytoplankton (0.10), kelp detritus (0.15), and detritus (0.15). They are consumed by Dungeness crabs, predatory invertebrates, some pelagic reef fish, and other demersal reef fish, depending on the life stage.

Large zooplankton

This group is comprised primarily of mesozooplankton, ichthyoplankton, and invertebrate larvae. Parameter estimates of $B = 16.3$, $P/B = 15.8$, and $Q/B = 45.6$ were based on the average for similar groups from other studies (67-69, 97).

Diet: A somewhat arbitrary diet was defined, dominated by phytoplankton (0.60), with contributions from small heterotrophs (0.25), kelp detritus (0.10), and cannibalism (0.05).

Small heterotrophs

This group includes all heterotrophic organisms less than 200 μm in size. Estimates of $B = 11.7$, $P/B = 125$, and $Q/B = 290$ were based on the herbivorous zooplankton groups defined by (68, 69). A diet dominated by phytoplankton (0.8), supplemented by kelp detritus (0.10) with equal (0.05) parts detritus and cannibalism was defined. Production and consumption estimates correspond well with those used by (66) for the microzooplankton group ($P/B = 100$, and $Q/B = 285$), however their $B = 5.3$ estimate based on $EE = 0.8$ was notably lower. The higher B value used here is justified under the assumption that the exposed coast is more productive than Puget Sound.

Phytoplankton

This group includes those organisms that synthesize organic compounds from CO₂ and nutrients through photosynthesis. Diatoms are the most common phytoplankton in temperate latitudes. Unicellular, but often existing in colonies as filaments, diatoms were once widely believed to be the base of the marine food chain, feeding copepods that were then consumed by fish. This view has evolved in recent years, and this diatom-copepod-fish food chain, while important, appears to be limited to periodic high-biomass diatom blooms (103).

Ecopath models are generally insensitive to phytoplankton B and P/B values since it is rarely modelled as a limiting resource. This model therefore initially used the average from the other 4 models of the region ($B = 25$, $P/B = 125$). Biomass was increased to $B = 28$ on balancing (see below).

Macroalgae

Because of the putative role of canopy (or overstory) kelps as nursery habitat, and the apparently different roles played by the dominant species (104), the canopy kelp were separated into the perennial giant kelp (*Macrocystis pyrifera*) and the annual bull kelp (*Nereocystis macrofoliata*). All other kelps were grouped into the other macroalgae group, recognizing that this is a large, diverse group.

Kelp production

Through a detailed review of bull kelp B and P/B , (66) concluded that the growth of individual sporophytes for rapidly growing species is better reflected in the P/B ratio, and not the B . Their $P/B = 43$ for bull kelp was accepted. For the perennial giant kelp, while potentially faster growing than bull kelp at its peak growth rate, turns over less biomass in a season. In a

study of giant kelp turnover in California, (105) provide estimates of both standing stock and production, from which a $P/B = 6.08 \text{ yr}^{-1}$ was estimated. The diverse other macroalgae group includes all other species of fleshy macroalgae, including corallines. A $P/B = 15 \text{ yr}^{-1}$ was assigned to a similar group in Puget Sound (66), and this value was adopted here.

Kelp biomass

Kelp B was difficult to estimate for the entire study area not only because localized field studies tend to be at the scale of an individual kelp forest, but also because of high inter-annual and across site differences. Habitat suitability models have been used to estimate presence/absence of kelp over large areas (e.g., (106)), and some studies have assumed general biogeographic distributions (e.g., (29)). However, no study was found that provided a rationale for estimating kelp biomass in a quantitative way from local data to a larger region. Here, field data collected from local sites with and without sea otters, regional data on kelp abundance, and assumptions about potential and realized habitat were assessed for their suitability for scaling the kelp B .

Given the variability in kelp sampling and the significant scaling challenges (73), Ecopath was allowed to estimate B with the understanding that the otter-absent system is dominated by grazers, a situation that leads to low B values and high EE . A higher EE also agrees with the earlier assumption that sea urchins are food limited. Assumed EE s of 10%, 90%, and 50% were used for bull kelp, giant kelp, and other macroalgae respectively. These values reflect the fact that bull kelp tends to be distributed in higher exposure areas or areas of higher current where it is less accessible to sea urchin predation. The other macroalgae group was assigned an intermediate value as some species in this diverse group are less likely to be eaten by grazers.

Kelp Detritus and Detritus

Biomasses for the detritus groups are used only for tracking relative change. The actual B values are based on the flows from the other groups. Both detritus pools were, according to standard practice, set to an arbitrary value of 10.0. All groups were directed to detritus except the three kelp groups, which were sent first to the kelp detritus pool.

Other Ecopath parameters

The unassimilated portion of consumption was changed from 0.2 to 0.4 for all the grazer groups in the model (sea urchins, large grazers, small grazers, meso-grazers, large zooplankton, and small heterotrophs) to reflect the likelihood that the assimilation rate of species and groups that are primarily herbivorous was lower than the default. *Ad hoc* sensitivity analyses suggested that the model was relatively insensitive to changes in this parameter.

5.2. Model balancing and tuning

All that was necessary to balance the model given the initial set of parameters described above was to raise primary production B from 25 to 28, a trivial change well within the acceptable range.

Model tuning in response to two derived ecological values led to one set of minor adjustments. Respiration (R), and food conversion efficiency (P/Q) provide a simple diagnostic for evaluating the realism of parameters in balanced models. Realistic P/Q values are expected to be on the range 0.1 - 0.3, with lower values for top predators and higher values for small organisms (e.g., to 0.5 for bacteria). Reasonable values for R range from 1-10 for fish and between 50 -100 for smaller organisms such as copepods (107).

P/Q values were low (< 0.1) for sea urchins, geoduck clams, and large grazers. Corresponding R values were quite high for urchins and large grazers, but appropriately low for

geoduck clam (even though the value is twice as high as other edible clams group, this could be explained by the energy required for nutrient pumping by deeply buried species). Thus, no adjustments were made to the geoduck clam parameters. Adjusting Q/B and P/B for sea urchins was considered, however the parameters were reliably derived, and sizable, perhaps unrealistic changes were required to bring the R and P/Q values within the recommended ranges. Given that the recommended ranges are intended primarily for fish species, and that sea otter values (assumed to be realistic) provide an example where species may fall outside these ranges, no adjustments were made to the parameters for these groups. It was assumed an R slightly < 1 was acceptable for bivalves given their sedentary nature.

An R of 0.72 for the other demersal reef fish group seemed low, though P/Q was acceptably in the middle of the fish range. Some experimentation was necessary to avoid unbalancing the model because this group is broadly trophically connected. Ultimately, both P/Q (0.24 \rightarrow 0.3 yr^{-1}) and Q/B (1.2 \rightarrow 2.0 yr^{-1}) were raised, giving a more reasonable (though not ideal) $R = 1.3$. This brought the base parameters more in line with lingcod, but produced too much B requiring a small reduction in EE (to 0.9) to balance the model.

5.3. Ecosystem dynamics

Ecosim's representation of ecosystem dynamics uses a number of observed phenomena that are difficult to parameterize. These include *vulnerability* — the density-dependent relationship between a predator and its prey, and *mediation* — the indirect change in production attributable to another species (e.g., biogenic habitat). These two essential parameters are discussed in detail below. For details on the remaining Ecosim parameters see (73).

Vulnerability is a predator-prey specific foraging parameter that relates to density-dependence. It can be interpreted as the amount a given predator could increase the predation

mortality it is causing on a prey species if the predator population reached carrying capacity. Thus, depleted populations will have high vulnerability exchange parameters (as defined by (108)), while populations close to their carrying capacity will have vulnerability close to 1. Vulnerability can be estimated with knowledge of a predator's current biomass and carrying capacity, but carrying capacity is generally unknown and estimates of population size are typically uncertain. Best practice is therefore to estimate vulnerabilities through time-series fitting (109). The estimation of vulnerability was facilitated by grouping the sea otter prey into three ecologically-based vulnerability classes (Table S5; see (73) for details). To estimate the increase in rockfish habitat due to kelp (a classic mediation effect, e.g., (97)) a standard mediation curve was used as recommended by (110).

Ecosim provides a time-series fitting routine, which estimates vulnerabilities by minimizing the differences between the trajectory of model populations and observed population trends. Data used to fit the vulnerabilities included a sea otter population trend based on decades of observational data (111), and two points for each sea otter prey species for which otter-absent and otter-present estimates could be made (Table S1).

Estimates of vulnerability and mediation contain uncertainty that is difficult to quantify. However, these parameters allow characterization of a foraging arena (108), which provides a more accurate representation of reality. Thus, despite uncertainty in these parameters, the inclusion of foraging arena theory leads to a better fit to the available data, and reduces overall model uncertainty.

Table S1. Primary Ecopath parameters. Production (P/B) and consumption (Q/B) rates, local, observed biomass (B, g·m⁻²) and proportional change (ΔB) from otter-absent to otter-present systems, B values scaled to the study area for the two sea otter states, and the source of the data. Values in italics were input to the Ecopath model. Biomasses for groups with no values listed in the Scaled-Absent column were estimated using an assumed ecotrophic efficiency (EE). Other model sources are described in the text. Shaded values were used to create the predicted time series used for vulnerability fitting and model assessment. See supplemental materials text for additional details and terminology.

Species/Group	P/B	Q/B	Observed B (g m ⁻² yr ⁻¹)		ΔB	Scaled B (g m ⁻² yr ⁻¹)		Source
			Absent	Present		Absent	Present	
Sea otter	<i>0.186</i>	<i>120</i>	89 ^a	8302	93.28	<i>0.000585</i>	0.0546	(65)
Sea urchin	<i>0.244</i>	<i>10.9</i>	2900	25	0.0086	29	0.250	(9)
Dungeness crab	<i>1.5</i>	<i>4.25</i>	--	--	--	--	--	EE Estimate
Geoduck clam	<i>0.048</i>	<i>2</i>	700	--	0.80	<i>70.0</i>	56.0	(89)
Mussels	<i>0.428</i>	<i>1.42</i>	82600	57100	0.69	<i>82.6</i>	57.1	(91)
Other edible clams	<i>0.41</i>	<i>1.37</i>	6462	--	--	<i>19.39</i>	--	(73)
Lingcod	<i>0.5</i>	<i>3.55</i>	--	--	--	<i>0.33</i>	--	Other models
Other demersal reef fish	<i>0.3</i>	<i>2</i>	--	--	--	--	--	EE Estimate
Pelagic reef fish	<i>2</i>	<i>10</i>	--	--	--	--	--	EE Estimate
Forage fish	<i>1.5</i>	<i>4.75</i>	--	--	--	--	--	EE Estimate
Kelp crab	<i>3.5</i>	<i>20</i>	--	--	--	--	--	EE Estimate
Predatory Invertebrates	<i>0.76</i>	<i>4</i>	60.0	50.6	0.84	<i>3.0</i>	2.5	This study
Large grazers	<i>0.4</i>	<i>10.1</i>	142	1.66	0.01	<i>7.2</i>	0.08	This study
Small grazers	<i>2</i>	<i>14</i>	19.5	65.8	3.37	<i>1.0</i>	3.29	This study
Meso grazers	<i>3.41</i>	<i>15</i>	39.1	7.67	0.20	<i>1.95</i>	0.38	This study
Sessile invertebrates	<i>2</i>	<i>13</i>	98.9	565	5.71	<i>4.94</i>	28.2	This study
Large zooplankton	<i>15.8</i>	<i>45.6</i>	--	--	--	<i>16.3</i>	--	Other models
Small heterotrophs	<i>125</i>	<i>290</i>	--	--	--	<i>11.7</i>	--	Other models
Phytoplankton	<i>125</i>	<i>0</i>	--	--	--	<i>28.0</i>	--	Other models
Bull kelp	<i>43</i>	<i>0</i>	--	--	--	--	--	EE Estimate
Giant kelp	<i>6.1</i>	<i>0</i>	--	--	--	--	--	EE Estimate
Understory kelp	<i>15</i>	<i>0</i>	--	--	--	--	--	EE Estimate

a. Introduced density of sea otters used to trigger the trophic cascade.

Table S2. Ecopath diet matrix. Predators are shown in columns, and their prey as rows. All columns sum to 1 representing the initial diet of all species groups except lingcod, which import 50% of their diet from outside the model system.

	Sea otter	Sea urchin	Dungeness crab	Geoduck clam	Mussels	Other edible clams	Lingcod	Other demersal reef fish	Pelagic reef fish	Forage fish	Kelp crabs	Predatory invertebrates	Large grazers	Small grazers	Meso grazers	Sessile invertebrates	Large zooplankton	Small heterotrophs
Sea otter	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sea urchin	0.45	0	0.05	0	0	0	0	0	0	0	0.01	0.02	0	0	0	0	0	0
Dungeness crab	0.05	0	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Geoduck clam	0.05	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mussels	0.1	0	0.05	0	0	0	0	0	0	0	0.2	0.2	0	0	0.01	0	0	0
Other edible clams	0.1	0	0.1	0	0	0	0	0	0	0	0	0.2	0	0	0.01	0	0	0
Lingcod	0	0	0	0	0	0	0.01	0	0	0	0	0	0	0	0	0	0	0
Other demersal reef fish	0	0	0	0	0	0	0.15	0.1	0.01	0	0	0	0	0	0	0	0	0
Pelagic reef fish	0	0	0	0	0	0	0.05	0.05	0.01	0	0	0	0	0	0	0	0	0
Forage fish	0	0	0	0	0	0	0.01	0.02	0.01	0	0	0	0	0	0	0	0	0
Kelp crabs	0.07	0	0.05	0	0	0	0.1	0.1	0.1	.03	0	0.02	0	0	0	0	0	0
Predatory Invertebrates	0.06	0	0.05	0	0	0	0	0.01	0.05	0	0.01	0.02	0	0	0	0	0	0
Large grazers	0.1	0	0.05	0	0	0	0	0.01	0.05	.01	0.01	0.02	0	0	0	0	0	0
Small grazers	0	0	0.05	0	0	0	0.06	0.05	0.05	0.05	0.06	0.2	0	0	0	0	0	0
Meso grazers	0	0	0	0	0	0	0.06	0.2	0.2	0.14	0.01	0.02	0	0	0.1	0	0	0
Sessile Invertebrates	0.02	0	0.34	0	0	0	0.06	0.25	0.05	0.01	0.2	0.2	0	0	0	0	0	0
Large zooplankton	0	0	0	0.01	0.01	0.01	0	0.2	0.42	0.75	0	0	0	0	0	0.3	0.05	0
Small heterotrophs	0	0	0	0.01	0.01	0.01	0	0.01	0.05	0.01	0	0	0	0	0.08	0.3	0.25	0.05
Phytoplankton	0	0	0	0.78	0.78	0.78	0	0	0	0	0	0	0	0	0.1	0.1	0.6	0.8
Bull kelp	0	0.2	0	0	0	0	0	0	0	0	0.1	0	0.01	0.01	0	0	0	0
Giant kelp	0	0.2	0	0	0	0	0	0	0	0	0.1	0	0.01	0.01	0	0	0	0
Understory kelp	0	0.2	0	0	0	0	0	0	0	0	0.1	0	0.2	0.15	0.1	0	0	0
Detritus	0	0.2	0.25	0.1	0.1	0.1	0	0	0	0	0.1	0.1	0.1	0	0.5	0.15	0	0.05
Kelp detritus	0	0.2	0	0.1	0.1	0.1	0	0	0	0	0.1	0	0.68	0.83	0.1	0.15	0.1	0.1

Table S3. Data quality for the main model parameters for each species or group. Each parameter was assigned a coefficient of variation corresponding to its data quality ranking for the re-sampling process (low = 0.80, medium = 0.40, and high = 0.20).

Species / group	Density (B)	Production (P/B)	Consumption (Q/B)
Sea otter	High	High	High
Urchin	Low	Low	Low
Dungeness crab	Medium	Medium	Medium
Geoduck clam	Medium	Medium	Medium
Mussels	Low	Medium	Medium
Other edible clams	Low	Medium	Medium
Lingcod	High	High	High
Other demersal reef fish	Low	Medium	Medium
Pelagic reef fish	Low	Medium	Medium
Forage fish	Low	Medium	Medium
Kelp crabs	Low	Low	Low
Predatory Invertebrates	Low	Medium	Medium
Large grazers	Low	Medium	Medium
Small grazers	Low	Medium	Medium
Meso grazers	Low	Medium	Medium
Sessile Invertebrates	Low	Medium	Medium
Large zooplankton	Low	Medium	Medium
Small heterotrophs	Low	Medium	Medium
Phytoplankton	Low	High	--
Bull kelp	Low	High	--
Giant kelp	Low	High	--
Other macroalgae	Low	High	--

Table S4. Scaled average catch rates for key commercial species. Average and standard deviation of the annual (1983 - 2008) catch of the 5 commercial species explicitly included in the trophic model for Fisheries and Oceans statistical areas 23 through 26. Catches are scaled to a catch rate based on the 4112 km² study area. This served as the fishing mortality in the otter-absent Ecopath model. Lingcod was scaled by an additional 0.10 to account for the majority of the catch occurring deeper than our study area.

Species	Mean annual catch (tonnes)	Standard deviation	Catch rate (t km⁻² yr⁻¹) Otters absent
Sea urchin	200	116.5	0.049
Crab	251	102.7	0.061
Geoduck clam	806	563.2	0.196
Other clams	297	211.2	0.072
Lingcod	124	701.6	0.030

Table S5. Vulnerability classes. Classification of functional groups into vulnerability classes based on understanding of ecological role and interaction with sea otters.

Species/Group	Accessibility	Value	Vulnerability
Urchin	High	High	
Large grazers	High	High	1000
Dungeness crab	High	High	
Mussels	High	Moderate	400
Geoduck clam	Low	High	200
Other edible clams	Moderate	Moderate	
Kelp crabs	Moderate	Low	
Predatory Invertebrates	High	Low	100
Sessile Invertebrates	High	Low	

Results tables

The following tables contain the quantitative values for the figures in the main manuscript and include: the predicted median change in dollar value of the services considered (Table S6) from otter-absent to otter-present system; the predicted change in annual landed value for commercial species (Table S7), and the predicted change in biomass for all functional groups in the Ecosim model (Table S8).

Table S6. Change in value of modeled ecosystem services. Median change in value (millions of 2018 CA\$) of ecosystem services on the West coast of Vancouver Island due to the transition from a sea-otter absent, urchin dominated system to an otter-present, kelp-dominated system. Predictions include estimates of key uncertainties for each service, shown as the 5th and 95th percentiles.

Service	5th %	Median	95th %
Direct catch	-10.34	-7.32	-4.65
Supplemental catch	2.03	9.37	30.38
Carbon sequestration	0.52	2.20	7.29
Tourism	20.74	41.53	66.62

Table S8. Changes in biomass of modeled groups. Relative change (ΔB) in biomass values ($g \cdot m^2$) from an otter-absent to an otter-present state by trophic group.

Trophic Group	Otter-absent	Otter-present	ΔB
Sea otter	0.00	0.04	93.79
Urchin	29.0	0.05	1.60×10^{-03}
Dungeness crab	0.07	1.49×10^{-09}	2.28×10^{-08}
Geoduck clam	70.0	52.76	0.75
Mussels	82.7	68.41	0.83
Other edible clams	58.2	13.81	0.71
Lingcod	0.33	1.01	3.01
Other demersal reef fish	2.83	4.16	1.47
Pelagic reef fish	0.23	0.36	1.59
Forage fish	0.11	0.15	1.32
Kelp crabs	0.87	3.17	3.62
Predatory invertebrates	3.01	4.72	1.57
Large grazers	7.18	0.44	0.06
Small grazers	2.13	6.35	2.98
Meso grazers	1.93	3.12	1.62
Sessile invertebrates	4.99	4.22	0.85
Large zooplankton	16.52	19.24	1.17
Small heterotrophs	11.72	12.65	1.08
Phytoplankton	27.80	26.47	0.95
Bull kelp	14.94	18.22	1.22
Giant kelp	11.95	156.19	13.07
Other macroalgae	7.28	35.54	4.88
Detritus	9.62	10.26	1.07
Kelp detritus	10.95	19.54	1.78
Total	335.57	460.90	1.37