Representing mediating effects and species reintroductions in Ecopath with Ecosim

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ABSTRACT

Ecosystem models play an important role in supporting ecosystem approaches to management. To improve the representation of how ecosystems work, ecosystem models should be able to represent mediating effects (e.g., habitat provision) that species provide to each other as well as species (re)introductions, both common situations that can strongly influence ecosystem dynamics. We examine how such processes can be incorporated into Ecopath with Ecosim (EwE), a widely used tool for representing aquatic ecosystems with the potential to support ecosystem-based management. We used the reintroduction of sea otters (Enhydralutris) to the west coast of Vancouver Island, British Columbia, Canada as a case study. The model demonstrates how to account for benefits provided by kelp forests by contributing to primary production, increased feeding areas and food availability through prey retention. It also demonstrates how the reintroduction and range expansion of sea otters can be represented in Ecospace, and the implications of these options.

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1. Introduction

Ecosystem models play a fundamental role in ecosystem-based management (EBM). They can improve our understanding of complex systems and allow us to represent the trophic and non-trophic interactions between multiple species within an ecosystem. They do this while accounting for the impacts of environmental forcing factors (e.g., Heymans, 2005b), human activities (e.g., Pauly et al., 2000), and protected areas (e.g., Walters et al., 1999). They can also support scenario analysis (e.g., Christensen and Walters, 2004b) by predicting policy outcomes and the impacts of environmental change (Christensen and Walters, 2004a,b).

To make ecosystem models widely applicable for EBM, they should account for the wide range of societal objectives as well as technical and ecological processes (see FAO, 2008). This analysis focuses on how to improve the representation of ecological processes, specifically the mediating effects provided by habitat and the spatial representation of species (re)introduction (e.g., reintroduction of extirpated species, or the arrival of exotic species) and expansion. These ecological effects have been shown to have notable impacts on community structure and dynamics (e.g., Dill et al., 2003; Gurevitch and Padilla, 2004).

Mediating effects can amplify or counteract predator–prey relationships, facilitating or inhibiting risk to predation and competition for food and space (Dill et al., 2003; Heithaus et al., 2008) sometimes overshadowing direct predation mortality (Heithaus et al., 2008). For example, kelp forests provide refuge for juvenile fish, reducing their risk to predation (negative effect for predators of juvenile fish). Kelp forests may also increase food availability for some predators through prey retention. Despite the recognition that such mediating effects are important (Heithaus et al., 2008; Wabnitz, 2010) they have been largely overlooked in ecosystem models (Dill et al., 2003; Heithaus et al., 2008). Species introductions can also induce dramatic changes to ecosystems, such as the observed trophic cascade caused by the re-introduction of sea otters (Enhydralutris) to the west coast of Vancouver Island (WCVI), British Columbia, Canada (Watson, 1993) or the arrival of green crab (Carcinusmaenas) to Bodega Bay Harbour, California (Grosholz et al., 2000). Thus, correctly representing the dynamics resulting from the addition of a species to an ecosystem is critical to better understand the changes in the system and to develop ecosystem management strategies.

Here we examine how to represent these dynamics (mediating effects and (re)introductions) in Ecopath with Ecosim (EwE), a widely used software for representing aquatic ecosystems.
Fig. 1. Reintroduction site (star), current range (grey) and sites with optimum habitat (black) for sea otters based on intertidal complexity similarity with the reintroduction site (Gregg et al., 2008). Published with the permission of the authors.

(Christensen and Walters, 2004a,b). The popularity of EwE is at least partially due to its user-friendly interface and continued improvements to the software (Plagányi, 2007). EwE remains the most popular tool for exploring the impacts of fisheries on ecosystems (Plagányi, 2007) and has been recommended for supporting EBM (Kaufman et al., 2009).

EwE represents mediating effects using a ‘mediation’ function. However, despite the importance of these effects and the ability to represent them, there is only a few examples of incorporating these effects into ecosystem models (e.g., Fulton and Smith, 2004; Wabnitz, 2010; Walters et al., 2010). To encourage the use of this functionality, we demonstrate how it can be used and implications in Ecosim and Ecospace. We also explore how to represent species (re)introductions and range expansion in Ecospace, which does not yet allow such representation: Ecospace currently assumes that all populations are distributed across the whole area in the initial state of the ecosystem (Christensen et al., 2008). We demonstrate how to model such dynamics using the re-introduction of sea otters to nearshore ecosystems on the west coast of Vancouver Island (WCVI) as a case study.

1.1. Case study

Sea otters were extirpated from British Columbia, Canada by 1930 (Watson, 1993) due largely to the intensive international fur trade between the 17th and 18th centuries (Estes and Smith, 1978). In the 1970s, sea otters were re-introduced to British Columbia on the WCVI where they have since successfully re-established themselves (Watson, 1993; Nichol et al., 2009). They reached carrying capacity in the central portion of their range and their expansion continues, particularly to suitable habitats (Fig. 1) along the WCVI (Gregg et al., 2008).

Sea otters are widely regarded as a keystone species, able to restructure nearshore marine environments from an invertebrate—primarily sea urchin—dominated system into a kelp-dominated system (i.e., ‘kelp’ species Macrocystis integrifolia, Nereocystis luetkeana) (Estes and Palmisano, 1974; Simenstad et al., 1978) by releasing the kelp from grazing pressure (Estes and Palmisano, 1974).

Kelp forests provide a number of important ecological benefits to nearshore ecosystems (e.g., Duggins et al., 1990; Markel, 2006).

Fig. 2. Food web of the nearshore ecosystem on the WCVI. Trophic interactions adapted from Simenstad et al. (1978), Halpern et al. (2006), Markel (2006) and Markel (pers. comm.). All lines represent trophic interactions between species. Dashed lines represent the hypothetical prey–predator relationships affected by mediating effects provided by kelp forests (i.e., increased feeding areas and food availability through prey retention). TL means trophic level.
Fig. 3. Culling scenario, with one suitable habitat. To simulate the sea otter reintroduction, we worked around the Ecospace’s assumption on the initial distribution of biomass. Sea otter biomass (in grey) was assigned to all the cells in the map, one marine protected area (MPA) was set in the first cell and a cull in the form of high fishing effort for the first 10 years in the 29 remaining cells. The intention was to concentrate sea otter biomass in cell 1 and drive the population down to 0 in the rest of the cells.

Table 1
Basic inputs for Ecopath. B means biomass, P/B production per unit biomass and Q/B consumption per unit biomass.

<table>
<thead>
<tr>
<th>Functional groups</th>
<th>B (t/km²)</th>
<th>P/B (year⁻¹)</th>
<th>Q/B (year⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sea otters</td>
<td>0.127</td>
<td>0.15</td>
<td>75.00</td>
</tr>
<tr>
<td>Lingcod</td>
<td>0.005</td>
<td>1.00</td>
<td>3.30</td>
</tr>
<tr>
<td>Rockfish</td>
<td>1.50</td>
<td>0.18</td>
<td>3.36</td>
</tr>
<tr>
<td>Forage fish</td>
<td>15.83</td>
<td>0.60</td>
<td>8.40</td>
</tr>
<tr>
<td>Surperches</td>
<td>1.00</td>
<td>0.70</td>
<td>10.82</td>
</tr>
<tr>
<td>Crabs</td>
<td>8.00</td>
<td>3.00</td>
<td>10.90</td>
</tr>
<tr>
<td>Benthic invertebrates</td>
<td>43.00</td>
<td>1.90</td>
<td>12.70</td>
</tr>
<tr>
<td>Filter feeders</td>
<td>20.00</td>
<td>1.20</td>
<td>6.00</td>
</tr>
<tr>
<td>Sea urchins</td>
<td>30.00</td>
<td>0.40</td>
<td></td>
</tr>
<tr>
<td>Zooplankton</td>
<td>68.00</td>
<td>16.50</td>
<td>62.50</td>
</tr>
<tr>
<td>Phytoplankton</td>
<td>22.00</td>
<td>179.00</td>
<td></td>
</tr>
<tr>
<td>Canopy kelp</td>
<td>9.00</td>
<td>5.30</td>
<td></td>
</tr>
<tr>
<td>Understory kelp</td>
<td>18.00</td>
<td>5.30</td>
<td></td>
</tr>
<tr>
<td>Kelp detritus</td>
<td>0.11</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Detritus</td>
<td>10.00</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Parameters were adapted from Ainsworth et al. (2002), Martell (2002), Preikshot (2005), Heymans (2005a,b) and Froese and Pauly (2010).

We focus on the mediating effects of kelp forests due to the provision of complex habitat through its three-dimensional structure (Duggins et al., 1989), which can increase feeding areas and food availability for diverse species (Anderson et al., 1997). In addition, we account for kelp contribution to primary and secondary production (Duggins et al., 1990) – most of the net kelp production is captured by other organisms in the form of detritus or dissolved organic matter, a high quality source of carbon for many species (Duggins et al., 1989; Duggins and Eckman, 1997). Other potential benefits include increased larval retention, survival, and recruitment (Duggins et al., 1990; Eckman and Duggins, 1991).

The recovery of sea otters along the WCVI has created considerable controversy (Watson, 2000) because of the conflicting objectives in the region. For some stakeholders sea otters are a threat to species with high commercial and cultural value (Watson, 2000); for others, they represent a benefit in terms of ecosystem diversity and productivity or opportunities for fishery fisheries and the tourism industry (Markel, 2006; COSEWIC, 2007). Thus, as the sea otter population expands its range along the WCVI, a conceptual ecosystem model of this system can contribute to an integrated, science-based understanding of the ecosystem dynamics.

We built a theoretical ecosystem model using EwE to show how to incorporate fundamental ecological dynamics, specifically, we wanted to demonstrate: (a) the contribution of kelp-particulate detritus to primary and secondary production; (b) the mediating effects provided by kelp by increasing feeding areas and food availability for some species; and (c) the sea otter re-introduction and expansion across the study area showing these effects across space and over time.

Table 2
Diet compositions. Predators are listed in column heading, preys are listed in rows.

<table>
<thead>
<tr>
<th>Functional groups</th>
<th>Sea otters</th>
<th>Lingcod</th>
<th>Rockfish</th>
<th>Forage fish</th>
<th>Surperches</th>
<th>Crabs</th>
<th>Benthic invert.</th>
<th>Filter feeders</th>
<th>Sea urchins</th>
<th>Zooplankton</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sea otters</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lingcod</td>
<td></td>
<td>0.25</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Rockfish</td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Forage fish</td>
<td>0.01</td>
<td>0.50</td>
<td></td>
<td>0.02</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Surperches</td>
<td>0.01</td>
<td></td>
<td></td>
<td>0.15</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Crabs</td>
<td>0.35</td>
<td></td>
<td></td>
<td></td>
<td>0.25</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Benthic invertebrates</td>
<td>0.10</td>
<td>0.429</td>
<td></td>
<td>0.70</td>
<td>0.50</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Filter feeders</td>
<td>0.30</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.20</td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Sea urchins</td>
<td>0.33</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.30</td>
<td>0.30</td>
<td>0.20</td>
<td>0.50</td>
</tr>
<tr>
<td>Zooplankton</td>
<td>0.30</td>
<td>0.90</td>
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<td>0.50</td>
<td></td>
<td></td>
<td></td>
<td>0.10</td>
</tr>
<tr>
<td>Phytoplankton</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.30</td>
<td>0.30</td>
<td></td>
<td>0.20</td>
</tr>
<tr>
<td>Canopy kelp</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.30</td>
<td>0.30</td>
<td></td>
<td>0.20</td>
</tr>
<tr>
<td>Understory kelp</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.30</td>
<td>0.30</td>
<td></td>
<td>0.20</td>
</tr>
<tr>
<td>Kelp detritus</td>
<td>0.10</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.20</td>
<td>0.20</td>
<td></td>
<td>0.50</td>
</tr>
<tr>
<td>Detritus</td>
<td>0.49</td>
<td>0.40</td>
<td></td>
<td>0.70</td>
<td>0.40</td>
<td>0.05</td>
<td>0.05</td>
<td>0.05</td>
<td>0.49</td>
<td></td>
</tr>
</tbody>
</table>

Parameters were adapted from Ainsworth et al. (2002), Martell (2002), Preikshot (2005), Heymans (2005a,b) and Markel (unpublished data). Diet compositions add to 1.
Table 3
Results from 100 runs of the individual-based model (IBM), each region includes four cells except for region 1 which includes only one cell. Cell 1 represents the area where sea otters were reintroduced.

<table>
<thead>
<tr>
<th>Region</th>
<th>Cells included</th>
<th>Average predicted biomass (t/km²)</th>
<th>Standard deviation (t/km²)</th>
<th>Coefficient of variation</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>1</td>
<td>0.1530</td>
<td>0.0136</td>
<td>0.0888</td>
</tr>
<tr>
<td>2</td>
<td>2, 3, 4, 5</td>
<td>0.1510</td>
<td>0.0093</td>
<td>0.0616</td>
</tr>
<tr>
<td>3</td>
<td>6, 7, 8, 9</td>
<td>0.0893</td>
<td>0.0392</td>
<td>0.4558</td>
</tr>
<tr>
<td>4</td>
<td>10, 11, 12, 13</td>
<td>0.0917</td>
<td>0.0421</td>
<td>0.4591</td>
</tr>
<tr>
<td>5</td>
<td>14, 15, 16, 17</td>
<td>0.0935</td>
<td>0.0408</td>
<td>0.4364</td>
</tr>
<tr>
<td>6</td>
<td>18, 19, 20, 21</td>
<td>0.0857</td>
<td>0.0361</td>
<td>0.4212</td>
</tr>
<tr>
<td>7</td>
<td>22, 23, 24, 25</td>
<td>0.0786</td>
<td>0.0459</td>
<td>0.5840</td>
</tr>
<tr>
<td>8</td>
<td>26, 27, 28, 29</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>1–29</td>
<td>0.0972</td>
<td>0.0003</td>
<td>0.0309</td>
</tr>
</tbody>
</table>

Fig. 5. Results with and without the ‘mediation’ function in Ecosim. Species biomass over a 100-year period. Solid lines show the results with the mediation function which represents the effect of increased feeding areas and more vulnerable prey to some predators. The dotted lines show the results without mediation.

2. Methods

We used the three modules of EwE version 6 (EwE6) to represent the ecological dynamics. We developed the mass-balanced ecosystem in Ecopath, and therein demonstrated the contribution of kelp to primary and secondary production. We used Ecosim to represent the mediating effects using dynamic simulations, and Ecospace to explore how the re-introduction and expansion of sea otters occurred over time.

2.1. Ecopath parameterisation

Our conceptual food web (species and interactions) contained 14 functional groups consisting of the nearshore, commercially and ecologically important species (Fig. 2) most likely to be affected by sea otters (e.g., sea otter prey, kelp grazers). This food web was adapted from Simenstad et al. (1978), Halpern et al. (2006), Markel (2006), and Markel (pers. comm.).

We parameterized our model for the WCVI using data from previous EwE models built for Pacific waters of Canada and Alaska (i.e., Ainsworth et al., 2002; Martell, 2002; Preikshot, 2005, 2007; Heymans, 2005a,b) and existing databases (Markel, 2009, unpublished data). Initial Ecopath parameters and diet compositions are summarized in Tables 1 and 2 respectively.

We modeled the contribution of kelp to primary and secondary production by adding a functional group for kelp-derived detritus. Detritus groups in EwE6 represent all the biomass not eaten, but retained in the system and decomposed into organic matter. By
adding a detritus group specifically for kelp we ensured that this
group captured all the kelp detritus, allowing us to track its use. We
then linked the kelp detritus group to the canopy and understory
kelp biomass and included it in the diets of filter feeders (Duggins
and Eckman, 1997), benthic invertebrates, sea urchins (Duggins
et al., 1989; Markel, 2006), forage fish (e.g., Hand and Berner, 1881)
and zooplankton (Markel, 2006; Markel, pers. comm.).

2.2. Mediating effects in Ecosim

We used the Ecosim mediation function to model how kelp aug-
mented feeding areas and food availability for particular species
due to prey retention. The mediation function allows the explicit
representation of the effects of one species/group in facilitating
or inhibiting prey–predator relationships of two other species. By
default, it affects the trophic flow rate (TFR)—the biomass per time
step consumed by a predator (Christensen et al., 2008), defined as
follows:

\[
TFR = \left( \frac{a'_{ij}}{A_{ij}} \right) \cdot V_{i,j} \cdot P_j
\]

where \(a'_{ij}\) is the effective area searched by each unit of predator \(P_j\)
for prey per unit time, \(A_{ij}\) is the foraging area used by predator \(j\)
to feed on prey \(i\), \(V_{i,j}\) is the vulnerable prey biomass per unit area, and
\(P_j\) is the effective predator abundance per unit area. The vulnerable
prey biomass \(V_{i,j}\) is defined by an exchange rate \((v_{i,j})\), which gives
the proportion of the total prey biomass vulnerable to predator \(j\)
(Walters et al., 1997; Christensen et al., 2008). \(V_{i,j}\) is the calculated
using the following formula:

\[
v_{i,j} = \frac{(v_{i,j} \cdot B_i)}{(2v_{i,j} + a_{ij}'/A_{ij} - P_j)}
\]

where \(v_{i,j}\) is the vulnerability exchange rate and \(B_i\) is the biomass
of the prey. \(v_{i,j}\) is the defined for each prey–predator relationship
to represent how the biomass of different groups is controlled in
the system (top–down or bottom–up). Low \(v_{i,j}\) (close to 1) indicates
the prey only becomes vulnerable to predation when it leaves its
refuge. High \(v_{i,j}\) (e.g., 100) indicates the prey has no refuge and is
easily encountered by its predator, meaning that predator biomass
defines how much is eaten of a prey (top–down) (Christensen et al.,
2008). For our model, we kept the default \(v_{i,j}\) value of 2.0, except for
sea urchins eaten by sea otters (sea urchins are believed to be easier
capture by sea otters compared with other prey) and kelp forests
eaten by sea urchins. Both were set to 10.0. We did a sensitivity
analysis for \(v_{i,j}\) of sea urchins eaten by sea otters—using the values of
5, 10 and 20—to explore the effects on the results of changing
this parameter.

Eq. (2) is substituted in Eq. (1) to calculate the TFR. The media-
tion function uses multipliers from 0 to 1 to affect the parameters
\(a_{ij}', A_{ij}\) and \(v_{i,j}\). In EwE6, the relationship between the multiplier
and the biomass of the mediating organism can be defined graphi-
ically or selected from four different relationships (linear, sigmoid,
hyperbolic and exponential). Up to five mediation functions per
prey–predator relationship can be included (Christensen et al.,
2008).

In our model, we applied only one type of mediation using
a multiplier to change the parameters \(A_{ij}\) and \(v_{i,j}\) together. This
was done to represent that in the presence of kelp, some species increase their foraging areas or feeding areas \((A_{ij})\) in which the vulnerable biomass of some prey \((V_{ij})\) becomes more available. We assumed a sigmoid relationship between kelp biomass and the multiplier, meaning that increased kelp biomass will increasingly affect the multiplier until a point where kelp biomass will not make significant changes in the multiplier. We define hypothetical TFRs or prey–predator relationships affected by the mediation function (Fig. 2) based on Markel (2006). These hypothetical TFRs were reviewed and confirmed by ecologists familiar with the system (Markel and Martone, pers. comm.). To see the role of mediation in the ecosystem we ran the model for 100 years, and compared the results with and without mediation.

One observation for the analysis of mediating effects is that they cannot be observed in Ecosim when a model does not have any drivers that change the Ecopath initial condition (e.g., catch, fishing effort, biomass accumulation assumed from outside the map). In such cases, when the mediation is applied after year 1—once the model is balanced—all species are at equilibrium and Ecosim shows no change in the species biomasses for the subsequent years. Thus, for these cases, spatial representation (Ecospace) is necessary to observe the mediating effects.

2.3. Spatial representation of sea otter reintroduction and expansion: Ecospace structure

Sea otters were reintroduced in a single location on the WCVI and after 40 years re-established themselves in the area of reintroduction and continue to expand along the coast. To correctly represent this ecological history, we wanted our model to demonstrate how the reintroduction of sea otters to one specific area (i.e., one cell) can lead to their expansion across the whole study area.

To explore this dynamic in Ecospace, we began with a linear map defined by a single row of 30 \(10 \times 10 \text{ km}^2\) cells. This map hypothetically represents almost 300 \(\text{km}^2\) of the nearshore ecosystem on the WCVI, a region that includes both the area where sea otters were reintroduced, and the areas into which they are expanding (Fig. 1).

On initialization, Ecospace distributes the initial biomass assigned to functional groups (in Ecopath) evenly across all cells of the map. When habitat types are defined, Ecospace concentrates high biomass in suitable habitats and low biomass in unsuitable habitats. The underlying assumption in such cases is that the biomass in the unsuitable habitats will move rapidly to suitable habitats according to a ‘mixing’ rate per cell based on the dispersal rates, food availability, and vulnerability to predation of each cell (Christensen et al., 2008). By assigning some biomass to all cells, Ecospace is at odds with the concept of (re)introductions. In Ecospace, the only way to have 0 biomass for a species is to be driven to 0 by predation or fishing pressure.

We therefore created a Culling scenario to work around the assumption of initial species distribution in the system. We defined the whole area as a single suitable habitat for sea otters, and defined cell 1 (the northernmost cell) as a marine protected area (MPA). We then culled sea otters with high fishing effort (10 times the initial landings of 0.015 ton/km\(^2\)/year) for the first 10 years of a 100-year simulation (Fig. 3) in the remaining 29 cells. In this way we retained the sea otter biomass in cell 1, and drove the population to 0 in cells 2–30. We assumed that after 10 years the population in cell 1 would be the only surviving one, and that it would become the source of the expansion to the other cells.

In Ecospace, species move across cells using a mixing rate, which is assumed to be equal across cells (non including land cells) by
Fig. 8. Populations dynamics in a 100-year period. Results in Ecospace. Filled triangles represent the results with the diffusion model and filled circles the results with the Individual based Model (IBM). The dotted lines were only added to show the trends.

Fig. 9. Spatial distribution of sea otters using the Culling scenario using three different dispersal rates and the two types of models on Ecospace: Diffusion and Individual based Model (IBM). Yr represents the years of the results. Blue represents low biomass and red high biomass. The results of IBM were taken from a one run. This map has 30 cells from north (left side) to south (right side) used to represent the system spatially. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)
of 10 years. We then analyzed the results in intervals of 1 and 4 km). We then analyzed the results in intervals of 2 and 4 km for invertebrates and 1 km/yr for invertebrates and fish populations and 1 km/yr for invertebrates and primary producers. To explore how sensitive the results were to dispersal rates we ran the model with three different dispersal rates for sea otters. 

We ran Ecospace using two stanzas (juveniles and adults) for sea otters and fish populations and 1 km/yr for invertebrates and 2 km/yr for invertebrates and fish populations and 1 km/yr for invertebrates and primary producers. To explore how sensitive the results were to dispersal rates we ran the model with three different dispersal rates for sea otters (1, 2 and 4 km). We then analyzed the results in intervals of 10 years.

To analyze the stochasticity of the packets’ movement in IBM, we divided the study area into eight regions (Table 3). We ran the model 100 times and examined the results by calculating the average biomass, standard deviation, and coefficient of variation for sea otters per region using year 100 of all runs. We also ran the model with and without land limits around the map to examine if diffusion from outside the modeled area could be influencing the sea otter expansion. Finally, we compared the results obtained from Ecosim with those from Ecospace, to examine how the spatial representation influenced the predicted sea otter recovery.

3. Results and discussion

3.1. Ecopath network analysis results

The network analysis of our food web demonstrates the interactions between species within the ecosystem (Fig. 4). Sea otters had negative effects on sea urchins and crabs due to predation and positive effects on canopy and understory kelp by releasing kelp from the sea urchin grazing pressure. This sea otter–urchin–kelp relationship has been demonstrated empirically in the Aleutian Islands, Alaska (Estes and Pal misano, 1974; Duggins et al., 1989) and the WCVI (Watson, 1993). The negative effects of sea otters on crab abundance have been less explored, but there is some evidence of crab population declines in Alaska as a result of increased sea otter abundance (Garshelis and Garshelis, 1984). Results also show positive impacts of sea otter abundance on lingcod and forage fish, previously described by Markel (2006).
indirect positive effects on benthic invertebrates and filter feeders by releasing the grazing pressure on kelp, an important food source for these groups. This is consistent with empirical observations (Duggins et al., 1989).

Sea otters negatively affected themselves due to intra-specific competition, which is likely to occur in regions where they have reached their carrying capacity (Gregg et al., 2008). Indirect negative effects were shown on surperches due to increased predation by lingcod, consistent with effects described by Markel (2006).

### 3.2. Benefits provided by kelp forests over time

Including kelp detritus as a functional group allowed us to analyze its contribution to primary and secondary production in the ecosystem. In the presence of sea otters, kelp forests, largely through kelp detritus, contribute to the biomass of benthic invertebrates, filter feeders and sea urchins (Fig. 4).

To assess the change in kelp and kelp detritus abundance as otters recovered, we compared the final biomass at year 100 with the biomass at year 20, the year of lowest sea otter abundance. Canopy kelp increased over 142%, understory kelp by almost 57% and kelp detritus up 77% after sea otters recovered. The eutrophic efficiency (the ratio of biomass flow out of a group to the biomass that flows in) of kelp detritus was 0.99 in year 1. This means that virtually all the kelp detritus produced is consumed. This could explain the limited increase of kelp detritus in subsequent years. Sea otters, kelp forests, and kelp detritus followed the same trend (Fig. 5) over the time period.

A dynamic not represented in the model is that sea urchins feed on kelp forest holdfasts often leaving much of the plant available for decomposition. This dynamic intensifies the negative impacts of sea urchins on kelp forest abundance and contributes more to the production of kelp detritus. Because this dynamic was not represented in the model, we may have underestimated the impact of sea urchins on kelp and kelp detritus produced by urchins.

The mediation function produced notable changes in the biomass of some functional groups (Fig. 5). For example, lingcod and rockfish biomasses were correlated with sea otter and kelp biomass. With the mediation function, the two fish populations decreased up to 26.5% and 11.4% respectively during the first 50 years of the simulation when sea otter and kelp biomasses were low, but recovered quickly with the return of sea otters. Benthic invertebrates’ biomass increased 24.0% with the mediation function due to the increased availability of kelp detritus and decreased predation from rockfish and lingcod, but only for the first 50 years when the biomass of these fish populations were low. Kelp detritus increased 29.2% due to decreases in some of its primary consumers such as forage fish (the first 50 years) and sea urchins (last 30 years). Sea urchins declined 27.6% in the last 30 years due to a slight increase in sea otter predation (1.5% between year 60 and 80). Other functional groups showed slight changes in abundance. For example, surperch biomass increased 3.4% during the first 50 years when lingcod predation was low. With the recovery of lingcod surperch biomass declined 5.4%. Crab biomass increased 3.3% due to the increased availability of prey (benthic invertebrates) and decreased predation by rockfish in the first 70 years. The decrease in zooplankton biomass (2.3%)—due to benthic invertebrates’ predation—contributed to the decrease in forage fish biomass (4.1%) and to increases in phytoplankton (2.5%), and detritus (1.9%) biomasses. Filter feeders increased (4.5%) due to the increase in kelp detritus and detritus. The total biomass increased in average 1.8% with the mediation function.

We only used one mediation function and applied it to hypothetical prey–predator relationships based on consultation with experts to show how to use it and the implications for the results. However, more mediating effects caused by kelp forests and other species may take place in the ecosystem. The identification of mediating effects and the extent to which these effects alter prey–predator relations are often hard to identify even with relevant empirical data. Modeling these effects requires numerous assumptions that will be reflected in changes of ecosystem dynamics—such as in this case lingcod and benthic invertebrates—accordingly, modelers should use caution when applying and interpreting these effects in ecosystem models.

Finally, the sensitivity analysis of sea urchin vulnerability showed that as vulnerability increased, the risk to urchins from sea otter predation increased and their biomass decreased. These changes are observed largely in the last 30 years (Fig. 6). With the mediation function, increased urchin vulnerability decreased the biomass of lingcod (up to 28.7%) and increased the biomasses of benthic invertebrates (up to 6.1%), filter feeders (up 8.7%), canopy kelp forests (up to 17.8%), understory kelp (up to 8.7%) and kelp detritus (up to 17.5%). Without the mediation function, the same species—except for lingcod and surperches—showed very similar sensitivity to changes in sea urchin vulnerability as with the mediation function. The changes due to mediation—measured as the ratio of mediation: no mediation results—were not significantly affected by increased vulnerabilities (Fig. 7), except for lingcod (decreased up to 30%), sea urchin (decreased up to 23%), benthic invertebrates (increased up to 6.5%) and kelp detritus (increased up to 6.6%). The magnitude of these changes decreased as the vulnerabilities increased. Changes were mainly observed in the last 30 years of the time period, when sea urchins declined due to increased sea otter predation.

### 3.3. Spatial representation of sea otter reintroduction and expansion

The Culling scenario effectively overcame the initial biomass assignment by Ecospaces to all cells. When using this approach in EwE models, modelers can use as a starting point the year in which the (re)introduction is represented, in this case year 20. This scenario is only a work-around for the initial Ecospaces distribution and expansion (Fig. 8). It is important to note that this approach assumes uniform (or influenced) biomass distributions. If using it for other systems, modelers should be cautious when interpreting the results.
When the two stanzas (sea otters juvenile and adults) were added to compare the diffusion and IBM movement models, the biomass produced by the IBM was more conservative than that from the diffusion model. This was because the IBM packets result in a wider range of organisms with different weights, leading to slower population growth (Fig. 8). The movement models represented the spatial expansion differently (Fig. 9). The diffusion model showed a graduated distribution of sea otters while the IBM model produced a more random distribution. At the end of the simulation, the biomass of sea otters in the diffusion model was concentrated in the first half of the map while the IBM show patches of high and low biomass across the study area (Fig. 9). This is due to the IBM packets random movement, with each following its own trajectory.

The sensitivity analysis of dispersal rates showed that increased dispersal rates make the dispersion faster (Fig. 9). However, changes in this parameter did not affect the way each model represented the expansion of sea otters and only slightly affected the total biomass of each functional group over time for the diffusion and IBM model (Fig. 10). The analysis of the influence of the randomization in the IBM showed high standard deviations and coefficient of variations in most regions (Table 3).

The diffusion model without the stanzas showed a faster expansion of sea otters than with the stanzas (Fig. 10). One reason for the more rapid movement is that Ecospace assumes a normal distribution of dispersal rates around the given value, allowing species biomass to move faster and slower than the given rate. Furthermore, the diffusion model does not distinguish the position that the functional groups have within a cell. Therefore, once a species occupies a cell, it can move to another one in the next time step, even if the cell is considerably larger than the stated dispersal rate.

The use of land limits demonstrated little difference in the species biomass results over time, except for surferches whose biomass variation was on average 1.6% with the diffusion, the rest of the functional groups variation was lower than 1%.

Our Culling scenario presented a way to model the reintroduction of a species to a specific region and its expansion across the whole study area. It helped avoid the assignment of biomass to the cells where 0 was intended. This scenario represents a work-around for an initial assumption of Ecospace. If the spatial representation of a species (re)introduction needs to be included in ecosystem models, modelers should be aware of this fundamental assumption and be cautious if using this type of scenario.

The two types of movement models (diffusion and IBM) demonstrated similar trends in the total biomass of functional groups for most cases but represented the sea otter expansion in two different ways. The diffusion model led to a graduated, more rapid dispersion while the IBM result in a slower, more heterogeneous distribution.

The comparison of the results obtained with Ecosim and Ecospace models showed that models that represent species exploitation and depletion spatially provide more conservative estimates of population growth and biomass than non-spatial models which assume widespread species with full access to vulnerable food sources (e.g., Ecosim models).

The model we built is theoretical. Therefore, the results are not suitable for marine planning processes in the region. Nevertheless, our model does represent key ecological dynamics and trends—empirically demonstrated by previous studies—such as the top-down cascade effects resulting from the re-introduction of a key-stone species. While our intent was to explore rarely used aspects of the EwE tool, our theoretical model nevertheless constitutes the first spatial model for the region (WCVI) and can serve as a foundation for future efforts. It has provided a structure for the integration of empirical information, helped identify data requirements, and evaluated alternative approaches for dealing with two important ecological processes not generally addressed by exiting models.

4. Conclusions

With this work, we showed how to represent mediating effects to EwE6 and species reintroductions in Ecospace, as well as their effects on the dynamics of a particular ecosystem.

We demonstrated how to account for kelp forest benefits by using an additional detritus functional group and the mediation function available in EwE6. The explicit accounting for kelp-derived detritus showed the contribution of kelp forests to primary and secondary production.

The use of the mediation function (i.e., increased feeding areas and food availability) show changes in biomass and sometimes opposite trends for some species (e.g., lingcod, rockfish and benthic invertebrates). Modelers have to make numerous assumptions when applying this function given that mediating effects and their magnitude are hard to predict even when having the empirical data. Therefore, the results derived from ecosystem models should be interpreted with caution.

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