From mountains to sound: modelling the sensitivity of Dungeness crab and Pacific oyster to land–sea interactions in Hood Canal, WA

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Many diagnoses of declining marine species and habitats along US coasts point to upland and freshwater sources of imperilment. Yet, little work has examined how and whether activities on land affect marine resources. Similarly, the impacts of climate change on coastal systems are among the most certain; yet, few studies have explored how alternative management and climate scenarios will affect the delivery of diverse benefits to people from coasts. We estimated how Dungeness crab (Metacarcinus magister) and Pacific oyster (Crassostrea gigas) harvest in Hood Canal, WA, may change given predictions of land uses and effects of climate change. These two marine species are critical components of local commercial and recreational fisheries and thus represent key “ecosystem service” endpoints. We found that Dungeness crab harvest responds strongly to effects of climate change, as mediated by increased ocean temperature, whereas Pacific oyster harvest is more responsive to projected change in land-use/land-cover due to increased nutrient loading to the marine system. These changes vary spatially throughout Hood Canal. These results can be used as a heuristic framework to help decision-makers, planners, and other stakeholders in the region as they work to target conservation and restoration activities and plan for future growth in a changing climate.

Keywords: climate change, Dungeness crab, future land use/land cover, land–sea interactions, marine water quality, Pacific oyster, scenario analysis, watersheds.

Introduction

Ever-increasing use of coasts and oceans by people is driving a need to develop plans and policies to accommodate multiple, and often conflicting, demands on those environments (Pew, 2003; Pikitch et al., 2004; McLeod and Leslie, 2009). Globally, 10% of the population (600 million people) lives in low elevation coastal zones that occupy only 2% of the land’s surface, and human migration to coastal regions continues (McGranahan et al., 2007). Managers and decision-makers are challenged to effectively craft strategies that address the current and projected needs of multiple sectors, which commonly include commercial and recreational fishing and shellfishing. Successful management strategies will be those that find a balance between uses and the capacity of the marine environment to support these uses, thus improving outcomes for the ecological system and for the human systems that depend on them (Lester et al., 2010; Eriksson et al., 2011).

Anthropogenic effects in the nearshore marine environment are direct (e.g. commercial fishing) and indirect (e.g. excessive nutrients in agricultural run-off or leaching from septic systems affecting coastal water quality) and can often be driven by land-based
processes (Díaz and Rosenberg, 2008; Klein et al., 2010; Deegan et al., 2012; Klein et al., 2012; Maina et al., 2002). In addition, coastal habitats are affected by a changing climate from both terrestrial and marine sources (Nicholls et al., 2007; Rosenzweig et al., 2007). From the terrestrial side, climate-associated changes in temperature and precipitation affect soil moisture, ground water, hydrology, sediment supply, salinity, and run-off from watersheds into marine receiving waters (Bates et al., 2008). From the marine side, changes in sea level, currents, wave heights, and coastal storms exacerbate coastal erosion, flooding, and saltwater intrusion (Scavia et al., 2002). Together, these forces interact to alter the structure and functioning of coastal habitats. A growing number of scientists argue that the best hope for maintaining a broad range of marine ecosystem services into the future is to consider these larger scale, land–sea processes when designing ecosystem-based management strategies (USCOP, 2004; Arkema et al., 2006; Ruckelshaus et al., 2008; Levin et al., 2009; McLeod and Leslie, 2009; Lester et al., 2010). What is not clear from the perspective of a manager of marine resources is when land–sea interactions are expected to be important and when a simpler, marine-based strategy is likely to be sufficient.

Approaches offering concrete guidance are lacking on whether and where marine resource managers should target watershed-based pressures, and under what conditions nearshore strategies are sufficient to protect or recover recreationally, commercially, and culturally important marine species. An evaluation of the responses of marine species and nearshore processes to upland pressures and potential effects of climate change, especially in systems whose species are not heavily targeted by commercial fisheries, can help managers target protection and recovery strategies for focal marine species. These analyses are most informative when they are spatially explicit; many stakeholders, sectors, and thus management priorities are based on interactions with the marine system in specific places (Pittman et al., 2011). Spatially explicit analyses can be used to identify areas that are most vulnerable to watershed- and marine-based pressures. Providing this information to decision-makers can help identify which stakeholders or sectors will be most vulnerable and inform where to pursue proactive management for those vulnerabilities or uncertainties. Also, such information can direct managers of marine resources to target engagement strategies with terrestrial decision-makers for more integrated management of activities that occur on land but have impacts on coastal systems.

For a case study, we modelled the sensitivities of Dungeness crab and Pacific oyster harvest in Hood Canal, WA, to changes in land use and large-scale ocean and climate drivers, as a way to illustrate how watershed processes can affect the marine environment. The Canal was a natural choice for this work because of the challenges facing managers and scientists as they try to untangle and address the sources and solutions to persistent low dissolved oxygen levels in portions of the Canal. We focused on Dungeness crab and Pacific oysters because these two species have important commercial, recreational, and cultural significance in the region. The specific objectives of this research were to (i) develop spatially explicit models that link run-off from terrestrial watersheds to the marine environment and (ii) use these models to evaluate the sensitivity of Dungeness crab (Metacarcinus magister) and Pacific oyster (Crassostrea gigas) to projected future changes in the system. Changes in surrounding watersheds based on the current trends are examined as well as terrestrial and marine effects of climate change (i.e. precipitation and sea surface temperature).

**Methods**

**Study region**

Hood Canal (the Canal) is a glacier-carved saltwater fjord that comprises the western-most portion of Puget Sound, WA (Figure 1). It is ~100 km long, has an average width of 2.4 km, mean depth of 53.8 m, and surface area of 385.6 km². The northern portion of the Canal is connected to Puget Sound, and a shallow sill restricts water exchange between the Canal and the main body of Puget Sound (Newton et al., 1995). The Canal’s drainage basin (2.7 million hectares) includes major rivers to the west (Skokomish, Hama Hama, Duckabush, Dosewallips, Big and Little Quilcene Rivers) that drain portions of the Olympic Peninsula and the Olympic National Park and smaller rivers to the east (Dewatto, Tahuya, Union Rivers) that drain portions of the Kitsap Peninsula. The region around the Canal is sparsely populated (~60,000 residents). Primary land uses include logging and a National Park on the Olympic Peninsula, along with rural residential use and protected wooded areas, limited agriculture, and a small amount of medium- and high-density development. The Canal’s beaches and tidelands support a lucrative commercial shellfish aquaculture industry for a variety of shellfish, including several species of oyster, geoduck, and Manila clams. Other popular recreational uses include shellfishing and crabbing. Water quality is of high concern to stakeholders in the Canal, as problems of persistent low dissolved oxygen in the Canal’s southern reaches, driven by nutrient inputs from naturally occurring and anthropogenic sources, have led to recurring fish kills (Fagergren et al., 2004).

**Linked watershed-marine models**

We developed or reparameterized four simple process models to estimate the influence of land use and climate change on (i) watershed discharge and nutrients, (ii) marine water quality, (iii) Dungeness crab populations available for harvest, and (iv) Pacific oyster populations available for harvest (Figure 2). The models are linked sequentially, such that outputs from one model are used as inputs to the next model (e.g. estimates of freshwater flow from watershed models are used as an input to a marine water quality model). We model Dungeness crab and Pacific oysters as representative marine species because they (i) are affected by (and, for oysters, can also affect) water quality, which may be linked to upland activities and (ii) are important species for commercial, recreational, and tribal harvest. We used the four linked models to evaluate two scenarios of future land use and climate change. A brief description of each of the four models follows.

**Watershed discharge and nutrients**

We modelled discharge and total nitrogen for the 153 perennial subwatersheds in Hood Canal based on spatial variation in hydrological factors, land and water use, and vegetation. To do this, we reparameterized a set of freshwater models available in the InVEST tool (Tallis and Polasky, 2009; Kareiva et al., 2011). These models have been applied in a variety of locations to assess how changes in climate and land use and cover influence water supply and nitrogen loading (Mendoza et al., 2011). We modelled discharge using the InVEST Water Yield and Scarcity model. The model estimates discharge for user-defined subwatersheds based on the average annual precipitation, annual reference evapotranspiration, and a correction factor for vegetation type, soil depth, plant available water content, land use and land cover, root depth, elevation,
Figure 1. Study area: Hood Canal, WA. Six areas included in the marine water quality model identified as boxes 1–6. Contributing watersheds are shaded for each box and major rivers within each contributing watershed are labelled. Circles indicate ORCA buoys; triangles indicate water quality mooring stations operated by WA DOE (Washington State Department of Ecology).
saturated hydraulic conductivity, and consumptive water use (Table 1; Mendoza et al., 2011; Tallis et al., 2011). The InVEST Water Yield and Scarcity model is a relatively simple hydrologic model that has been applied successfully in regions throughout the world, validated with regional observed data, and compared favourably with a more complex and widely used SWAT software program (output linear regression has an $R^2 = 0.824$; Ghide, Y.B.). We used the InVEST Nutrient Retention model to quantify the total nitrogen load for each subwatershed. Inputs to the Nutrient Retention model include water yield, land use and land cover, and nutrient loading and filtration rates (Table 1; Conte et al., 2011; Tallis et al., 2011). The nutrient model quantifies natural and anthropogenic sources of total nitrogen within each subwatershed, allowing managers to identify subwatersheds potentially at risk of contributing excessive nitrogen loads given the predicted development and climate future.

We calibrated the discharge model using annual stream data for 2005 through 2007 from ten USGS gages in ten of the modelled Hood Canal subwatersheds (USGS, 2011b). We calibrated total modelled nitrogen estimates using Washington Department of Ecology (WADOE) water quality data from six sampling stations in six of the ten subwatersheds used to calibrate the discharge model for the same period (WADOE, 2011a, b). Because WADOE data are monthly and the modelled nitrogen are annual, we used the LoadRunner software, which uses the USGS LOADEST program, to extrapolate an annual load of total nitrogen from the monthly WADOE concentration values using a regression model with daily time-series of streamflow (Booth et al., 2007). For both models, we averaged the observed annual water supply and the total nitrogen load for 2005, 2006, and 2007 to adjust the calibration factors used to calibrate the model.

The outputs of the Water Yield and Scarcity and Nutrient Retention models are average annual values. However, to link changes in land-use/land-cover and terrestrial aspects of climate change to marine resources, we needed to spatially and temporally link the freshwater results to the marine water quality model (described below). First, we spatially aggregated the subwatershed outputs for annual water supply (m$^3$) and annual total nitrogen load (kg) for a final sum for each of the six areas in the marine water quality model. To capture the seasonal variability necessary for the marine water quality model, we next proportioned the annual water supply and nitrogen load values in each box to monthly values based on the monthly averages of the observed data generated using LOADEST. We then re-expressed the monthly values as daily values based on the number of days in each month for input to the marine water quality model. In the final step, we reduced total nitrogen to nitrate based on the percent composition of nitrogen components in Hood Canal as reported in Steinberg et al. (2010). Our goal was to provide finer temporal resolution required by the marine water quality model and the proper nutrient component required to assess the influence of water quality on oyster and crab production.

The models do not include the influence of groundwater on surface water supply and nutrients, which may be another source of nitrogen loading to Hood Canal. We did account for the importance of out-of-basin water use that reduces the water supply to Hood Canal by manually reducing the water supply value by the appropriate amounts for each subwatershed for a total of ~40 million m$^3$. For additional information, Mendoza et al. (2011) and Conte et al. (2011) provide a thorough description and a series of case studies and analyses of the InVEST water yield, water scarcity, and nutrient retention models.

**Marine water quality model**

We used outputs from the freshwater models as inputs to the marine water quality model. We adapted a box model that has been successfully applied in Puget Sound (Babson et al., 2006; Sutherland et al., 2011) to simulate seasonal and interannual variations in salinity, water temperature, and nitrates in the Canal. We represented the Canal as six boxes (Figure 1), each divided into a surface and a deep box, which resulted in a total of 12 boxes. We estimated the depth of the surface box using observed salinity profiles. We estimated depth, area, and volume for each box from digitized bathymetry data (Finlayson, 2005). We determined initial conditions for salinity and temperature using observed data from five Oceanic Remote Chemical Analyzer (ORCA) buoy stations and at five WADOE mooring stations (Figure 1). We forced the model with daily quantities per month (e.g. 0.45 kg d$^{-1}$) for freshwater discharge and nitrate loads estimated from the watershed model. We defined oceanic conditions at the open boundary using the time-series of salinity and temperature observed at the point of exchange between the northern boundary of the Canal and the main stem of Puget Sound. We used the observed heat flux for surface temperature boundary conditions. The model output was a daily time-series

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**Figure 2.** Conceptual diagram of watershed-marine model linkages. Primary inputs and outputs of each model and temporal resolution of outputs are noted.
### Table 1. Watershed model inputs.

<table>
<thead>
<tr>
<th>Description</th>
<th>Spatial resolution</th>
<th>Timespan</th>
<th>Purpose</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Digital elevation model</td>
<td>30 m</td>
<td>1999</td>
<td>Hydrologic modelling</td>
<td>USGS (2011a)</td>
</tr>
<tr>
<td>Soil Depth</td>
<td>30 m</td>
<td>Varies with soil survey data</td>
<td>Depth to soil restrictive layer</td>
<td>SSURGO (2011) and STATSGO (2011)</td>
</tr>
<tr>
<td>Per cent available water</td>
<td>30 m</td>
<td>Varies with soil survey data</td>
<td>Per cent available water for vegetation</td>
<td>Derived from NRCS soil data using USDA Soil Viewer, an ArcGIS extension available at <a href="http://soils.usda.gov/sdv/">http://soils.usda.gov/sdv/</a></td>
</tr>
<tr>
<td>Precipitation</td>
<td>12 km</td>
<td>2035–2045</td>
<td>Predicted rainfall amounts</td>
<td>Maurer et al. (2007) and Girvetz et al. (2009)</td>
</tr>
<tr>
<td>Potential evapotranspiration</td>
<td>12 km</td>
<td>2035–2045</td>
<td>Predicted potential evapotranspiration</td>
<td>Maurer et al. (2007) and Girvetz et al. (2009)</td>
</tr>
<tr>
<td>Land use and land cover</td>
<td>30 m</td>
<td>2006</td>
<td>Vegetation and land use classes</td>
<td>Fry et al. (2011)</td>
</tr>
<tr>
<td>Land use and land cover</td>
<td>30 m</td>
<td>2040</td>
<td>Scenarios of future land use and land cover</td>
<td>Bolte and Vache (2010); Version 5</td>
</tr>
<tr>
<td>Zhang’s constant $= 9$</td>
<td>na</td>
<td>na</td>
<td>Characterize the seasonality of precipitation</td>
<td>Tallis et al. (2011) and best professional judgement</td>
</tr>
<tr>
<td>Plant evapotranspiration coefficient</td>
<td>na</td>
<td>na</td>
<td>Used to obtain potential evapotranspiration</td>
<td>Best professional judgement based on Allen (2003) and Bandaragoda et al. (2003)</td>
</tr>
<tr>
<td>Total nitrogen load</td>
<td>na</td>
<td>na</td>
<td>Nutrient load by land use class</td>
<td>Best professional judgement based on Reckhow (1980), Binkley et al. (1992), Compton et al. (2003), Sigleo et al. (2010), Paulson et al. (2004), and Steinberg et al. (2010)</td>
</tr>
<tr>
<td>Efficiency, total nitrogen</td>
<td>na</td>
<td>na</td>
<td>Nitrogen filtration by land use class</td>
<td>Nichols (1983), Hunter et al. (2009), Fredriksen (1972), and Correll et al. (1992)</td>
</tr>
<tr>
<td>Threshold flow accumulation value</td>
<td>na</td>
<td>na</td>
<td>Minimum threshold for stream based on GIS flow accumulation model</td>
<td>Regional, based on perennial hydrology, USEPA and USGS (2005), and best professional judgement</td>
</tr>
</tbody>
</table>

of temperature, salinity, and nitrates for use in the Dungeness crab and Pacific oyster harvest models. We summarized model outputs on a daily time-step so that we could evaluate temperature, salinity, and nitrate for distinct periods of the year (expressed as ranges of days) for Dungeness crab (i.e. planktonic larval phase) and model daily growth for Pacific oyster.

**Dungeness crab population available for harvest**

We modelled a population of Dungeness crab and its harvest with an age-structured, deterministic model coupled to a stock–recruitment relationship using a framework from Higgins et al. (1997). We used a Ricker curve to represent the stock–recruitment relationship, set the density-independent fecundity at the largest biologically reasonable value (2 million eggs), and assumed density-dependent production of eggs by 3- and 4-year-old females (McKelvey et al., 1980; Higgins et al., 1997). We excluded females older than age 4 due to reduced fecundity (Botsford and Wickham, 1978; Hankin et al., 1997). We modelled males and females separately because only males are harvested (vulnerable at age 4). We parameterized the model for the Canal by averaging values from along the US west coast for fecundity, survival estimates of larvae and adult crabs, and cannibalism of age 1 and 2 crabs (Higgins et al., 1997). As a harvest rate has not previously been determined for the Hood Canal Dungeness crab population, we adjusted an annual harvest rate for California, Oregon, and Washington (Higgins et al., 1997) to reflect only recreational and tribal harvest, since non-tribal commercial harvest does not occur in the Canal. Recreational and tribal harvest account for 61% of the total catch in Puget Sound (WDFW, unpubl. data). We estimated catch in the Canal to be 47% of age 4 males, which is 61% of the average catch value of 77.5% (WDFW, unpubl. data).
We linked the Dungeness crab production model to changing marine conditions by altering the survival of juvenile crabs in the planktonic and megalopa stage as a function of temperature and salinity as these life stages appear to be the most sensitive to temperature and salinity (Reed, 1969; Moloney et al., 1994; Holzman et al., 2006). We assumed crabs were planktonic from February until settling in mid-June (days of year 32–167; Pauley et al., 1989; Botsford and Hobbs, 1995). Using the same approach as Moloney et al. (1994), we produced survival estimates with the linear interpolation of temperature, salinity, and survival data from Reed (1969). Next, we adjusted crab survival estimates based on modelled temperature and salinity from the marine water quality model, average over the planktonic phase (days of year 32–167). The crab model accounted for differences in marine conditions with six separate production models—one for each section of the Canal in the marine water quality model. We assumed egg production was distributed evenly throughout Hood Canal and crab larvae settled in proportion relative to the surface area of each box.

Pacific oyster population available for harvest
We modelled farmed Pacific oyster populations in the Canal and their harvest by deterministically modelling individual Pacific oyster growth as a function of temperature and nitrate loading, adapted from Liddel (2008). We modelled oyster growth from outplanting to harvest, which meant that we assumed that the population was not recruitment limited, as spat and seed were assumed to be procured elsewhere for outplanting. The target harvest size was constant across the Canal, thereby not accounting for individual growers’ preferences for harvesting oyster of different sizes to fill variable demand in the half-shell and shucked oyster markets. The model ran on a daily time-step to accommodate seasonal changes in temperature and nitrates; both of these variables are generated in the marine water quality model and used as inputs to the Pacific oyster model. Outplanting occurred annually such that there was a mixture of different ages of oyster across the Canal. We scaled from the individual to the population level by calculating the density of harvestable oysters per unit area that would be required for modelled oyster harvest to fall within the range of observed 2004–2008 oyster harvest reported by the Washington Department of Fish and Wildlife (680 545–1 136 495 pounds).

Scenarios of future land use and climate change
We modelled the sensitivity of Dungeness crab and Pacific oyster harvest to projected land use and land cover and climate change through the following two scenarios.

Uncertainty
We show uncertainty in our results by modelling a range of inputs described below that reflect observed variability (i.e. in observed streamflows) or uncertainty about future conditions (i.e. testing future emissions scenarios). We also compared model outputs for the two scenarios to modelled baseline values, which reflect conditions in Hood Canal between 2005 and 2007.

Scenario 1: future land use and land cover
We evaluated a land use and land cover change scenario that was previously generated as part of a project to represent possible futures in Puget Sound (Bolte and Vache, 2010). The scenario was developed using the spatially and temporally explicit, multiple agent Envision modelling tool (version 5; Bolte et al., 2007; Hulse et al., 2008). We used Envision’s projected future land use and land cover under status quo conditions, where the assumption is that current trends (years 2005–2007 for this research) continue into the future (year 2040). Future land use and land cover was used as input to the watershed model, which led to changes in freshwater discharge and nitrogen loading to the marine system (i.e. to marine water quality model). We explored the sensitivity of model outputs under future land use and land cover to variable streamflow, by using the 25th and 75th percentiles of observed streamflows in gauged rivers throughout the Canal as model inputs in addition to the baseline average 2005–2007 streamflow.

Scenario 2: effects of climate change
To represent the effects of climate change on this system, we explored projected effects on precipitation, potential evapotranspiration, and oceanic temperatures for the years 2035–2045. We used Climate Wizard, a web-based program developed to visualize and access climate change maps and model outputs (Girvetz et al., 2009), to generate the future climate forecasts that served as inputs to the watershed model. In Climate Wizard, we averaged results from five of the most appropriate general circulation models for the Puget Sound region (CNRM-CM3, ECHAM5/ MPI-OM, ECHO-G, CGCM3.1-T47, and UKMO-HadCM3) for three emission futures (A1B, A2, and B1) to capture the range of potential variability in future conditions (Mote et al., 2008). These three modelled conditions represent the most frequent options used by the global modelling community for high, medium, and low global carbon emissions, respectively (Nakicenovic et al., 2000; Mote et al., 2008).

On the marine side, we explored the effects of a 1.5°C increase in water temperature in the outer boundary condition of the marine water quality model. Coastal sea surface temperatures in the Pacific Northwest are expected to increase in the 2040s by ~1.2–1.5°C based on the customized modelled output of Climate Wizard and Mote and Salathe (2009, 2010).

Results
Baseline conditions
Boxes 2, 4, and 3 received the highest modelled discharge (Figure 3a and c), due to high stream flow from the Skokomish (box 2), Big and Little Quilcenes and Dosewalps (box 4), Hamma Hamma and Duckabush (box 3) Rivers, and the large total area of contributing watersheds to those boxes. Boxes 2 and 3 both received disproportionately more discharge from contributing watersheds than other boxes; for example, while the watersheds that contributed to box 2 comprise 32% of all modelled watersheds in Hood Canal, discharge to box 2 contributed nearly half (46%) of total discharge to the Canal. Modelled freshwater discharge to the marine environment followed the observed seasonal cycle with high discharge in winter months and low discharge in late summer. The simulated discharge was closely related to the observed discharge from the ten watersheds with gauges on both a monthly ($R^2 = 0.996$) and annual ($R^2 = 0.999$) basis. Our simulated baseline discharge approximated observed data reasonably well; model estimates ranged from $-3$ to $+29%$ of the average observed discharge of the calibration watersheds.

The amount of total nitrogen estimated by the watershed model exhibited the same seasonal cycle as discharge, with the highest contributions to boxes 2, 3, and 4 (Figure 3b and d). However, while boxes 2 and 3 received proportionally more discharge than the area of their contributing watersheds, boxes 1, 5, and 6 all received...
larger proportions of total nitrogen relative to the area of their contributing watersheds. This indicates that the watersheds that contribute to boxes 1, 5, and 6 possess land use and land cover types with high nitrogen loading values (e.g. alders). The fit of the monthly simulated nutrient load to the monthly observed nutrient load was $R^2 = 1.0$ and the annual simulated nutrient load compared with the annual observed nutrient load was $R^2 = 0.995$ at the stream gauges.

Our simulated baseline estimates of nitrogen loads approximated observed data reasonably well for the larger subwatersheds and less accurately for the smaller subwatersheds. The simulated baseline total nitrogen load ranged from −49 to +53% of the average observed total nitrogen load of the calibration watersheds. However, in the largest watersheds, those that contain the Duckabush and Skokomish Rivers, the simulated loads were +16 and −3% different, respectively, from the observed values. This version of the calibration possessed the smallest range of difference from the observed value of each watershed, revealing the difficulty of calibrating small watersheds using discreet instantaneous monthly samples with potentially greater variability in concentration and discharge.

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were, as modelled for temperature and salinity, higher in surface boxes further south (i.e. far from the outlet of the Canal; Figure 4c and f). Box 1, which has the smallest surface area of any of the six boxes (9% of total area), had the highest modelled nitrate concentrations (40% of total annual average nitrates). This is likely due to higher contributions of total nitrogen from watersheds that flow to box 1 and the adjacent box 2, and circulation patterns that channel and contain nitrates to box 1, which has no outlet. Our model estimates of salinity fit observed values well ($r = 0.7$ for surface layer estimates; 0.9 for bottom layer estimates). The model was also able to reproduce the seasonal variability of salinity in the system. These results indicate that the model successfully simulated physical transport of mass in the Canal (Babson et al., 2006; Sutherland et al., 2011).

Given our approach to modelling crab harvest (proportional based on the box surface area), comparing absolute values of harvest across boxes is uninformative. However, boxes 5 and 6 had higher harvest proportional to their surface area due to more favourable temperature and salinity during the planktonic period (Figure 5a). We compared our estimates of Dungeness crab harvest with the observed average annual Dungeness crab harvest (1986–2011; WDFW, unpubl. data) for the entirety of Hood Canal. Our model results (449 263 crab) were within the range of observed harvest (observed: 370 889 crab ± 172 663 s.d.).

We used the Pacific oyster production and harvest model to estimate the annual harvest of Pacific oyster (pounds) in six areas modelled in the marine water quality model (Figure 5b). Modelled Pacific oyster harvest was highest in boxes 3 and 1, with lowest harvest in box 6. The total harvest for the Canal (945 834 pounds) fell within the range observed harvest (680 545–1 136 495 pounds) and harvest by box across the Canal followed the pattern of observed landings in the four reporting regions in the Canal.
Scenarios of future land use and land cover and climate change

Scenario 1: future land use and land cover

As modelled, future land use and land cover affected the total nitrogen that flowed into the Canal but did not affect the predictions of discharge. The watershed model estimated increases in total nitrogen from 11 to 73% for all boxes aside from box 1 (12% decrease); the highest increases were estimated for boxes 5 and 6 (Figure 6a). The variability in change in total nitrogen reflected differences in projected growth and change in land use and land cover between watersheds throughout the Canal. The decrease in the estimated total nitrogen in box 1 was due to the displacement of existing high nitrogen loading land use and land cover types with lower levels of nitrogen loading primarily associated with vegetation succession.

The change in total nitrogen, re-expressed as nitrates in the marine water quality model, resulted in changes to nitrates throughout the Canal (Figure 6b). Due to mixing and circulation patterns, estimates were muted when compared with those from the watershed models, such that nitrates decreased in box 1 (9% decrease) and increased in all other boxes (maximum increase of 28%).

Given uncertainty in future streamflow, we expressed uncertainty in our results by exploring sensitivity of model outputs to higher and lower discharges (25th and 75th percentiles of observed streamflows in gauged rivers) into the Canal. Lower discharges to the marine water quality model led to higher predicted nitrate levels throughout the Canal, as less freshwater was available to dilute the fixed volume of nitrates. Higher discharge had the opposite effect and led to decreased nitrate levels. In boxes 1, 2, and 3, however, higher discharge led to higher nitrate levels than observed in baseline conditions. This is, in part, because the baseline level of discharge was closer to the 75th percentile of all observed streamflow values than the 25th percentile and that increase to discharge varied by box (to reflect observed streamflows in one or more major rivers in each box).

The Pacific oyster model was responsive to changes in nutrients, which resulted in increased harvest (Figure 5b) for all boxes aside from box 1. There were no changes in Dungeness crab harvest because the Dungeness crab model did respond to changes in nitrogen.

Scenario 2: future land use and land cover and climate change

The forecast effects of climate change and ocean temperature led to changes in Dungeness crab as mediated by changes in the physical conditions in the watersheds and the Canal; land use and land cover changes alone did not affect crab harvest as the model was not sensitive to variables that changed under future land use and land cover (Figure 5a). The modelled changes were less pronounced for Pacific oyster (Figure 5b). Modelled discharge was higher in all boxes (maximum 32% increase in box 6) aside from box 1 (7% decrease; Figure 7a).
Results from B1 and A1B futures were similar, with slightly higher amounts of total nitrogen entering the Canal under the B1 emissions future; less total nitrogen and discharge enter the marine system under the A2 emissions future. Total nitrogen loading from the watersheds changed as reported for scenario 1, as there were no further changes to land use and land cover for scenario 2.

In the marine system, the influx of additional discharge diluted nitrates (Figure 7b). Without including effects of climate change, the maximum total increase in nitrates was 28% but was only 22% when effects of climate change (via additional precipitation) were included. The marine water quality model estimated changes in salinity of <0.5%. Finally, the 1.5°C increase in sea surface temperature led to increased sea surface temperature across the Canal (12–15%), with the highest increases in the northernmost boxes (Figure 7c).

For Dungeness crab, increases in temperature translated into higher juvenile survival which led to higher productivity within the population and supported higher harvests across the Canal (Figure 5a). While temperature increases were highest in the northern portion of the Canal, the percentage increase in harvest was highest in boxes 3, 4, and 1. Baseline temperatures during the planktonic period were lower in boxes 3, 4, and 1 than in the other boxes. While temperature increases were smaller in these boxes, these small increases had a proportionally larger effect on survival than the larger increases in boxes that already had higher temperatures.

For Pacific oysters, although temperatures and nitrates were higher than baseline, the additional discharge dampened the effect of additional nitrates (Figure 5b). The overall effect, regardless, was an increase in harvest, but less so than the increase in harvest in scenario 1.

Discussion
With a pressing need to understand how to manage land and sea in a more integrated way comes the need to develop approaches to understanding connectivity between the two systems (Tallis et al., 2008; Klein et al., 2012). Our approach helps advance land–sea modelling efforts by providing a framework to heuristically model sensitivities of marine ecosystem services to changes on land and in the ocean. There are strengths and limitations to the approach, which we discuss here, in addition to the potential utility of the approach for informing decision-making.

Our strategy for linking watershed and coastal/marine models was to build simple models that could replicate observed patterns well, had spatially explicit components, could be linked sequentially by passing outputs from one model to the next and could be used to evaluate scenarios of change on land and in the ocean. The advantage of this strategy is that it can be fairly easily adapted to other systems that have ecosystem services associated with crab and oyster (e.g. Chesapeake Bay on the U.S. East Coast; Galveston Bay, TX). None of the models require excessive amounts of input data or restructuring, and all can be easily reparameterized and calibrated given availability of observed data. Further, the models were not only constructed to characterize baseline conditions in the system, but use the production function approach (e.g. Kaiser and Roumasset, 2002; Ricketts et al., 2004), such that variables in each model respond to changes in input data. This enabled us to explore various scenarios to identify sensitivities in the two
models to future land and sea conditions. Scenario analysis is a powerful approach for moving beyond snapshot characterizations of a system because decision-makers can weigh results from a range of potential futures to better understand the robustness of their actions (Nelson et al., 2009; Guerry et al., 2012).

The simplicity of the framework has utility for developing integrated land–sea models but was intentionally designed to explore a limited set of connections within the system. In doing so, we excluded a suite of processes that may affect each model’s production function. Specifying production functions can often be challenging especially for land–sea systems, because data that can be used to comprehensively model responses of explanatory variables to various drivers are often scarce (Chan and Ruckelshaus, 2010; Alvarez-Romero et al., 2011). However, as a starting point, each model produced baseline outputs that fit observed values well, which gave us confidence that we modelled the baseline system well. As scientists learn more about cumulative effects of multiple drivers that affect outputs from each of our models, we can refine our production functions and increase confidence in our model predictions. Another avenue for improvement in linking the models is to more thoroughly model uncertainty and its implications as it propagates through the chain of models. As presented here, we conducted a limited exploration of uncertainty and variability in input data, but we could conduct a more rigorous analysis by using a simple Monte Carlo approach for a set of key parameters for each model. By modelling how uncertainty cascades from watersheds through marine ecosystem services, we can have higher confidence in our model outputs.

Our land use and climate change scenarios led to spatially variable changes in discharge, terrestrial-nitrates, and ocean temperature throughout the Canal, which resulted in similar patterns for Dungeness crab and Pacific oyster populations and harvest. Model outputs for both species indicated that they responded favourably to both scenarios. Dungeness crab juvenile survival increased with higher ocean temperatures, which drove increases in the population and its harvest. The modelled Pacific oyster population also fared well under conditions of future land use and land cover, with additional discharge from forecasts of higher precipitation and warmer ocean temperatures. The increase due to projected future land use and land cover was due to an influx of nitrogen from land into the Canal. Portions of the Canal are considered nutrient limited, so the additional nutrients led to higher productivity for the modelled Pacific oyster population and its harvest. When we included potential effects of climate change—via warmer ocean temperatures and increased precipitation—the higher temperatures were favourable for Pacific oyster growth and an increased population and harvest. Higher precipitation diluted some of the nitrogen, thereby offsetting some of the increases observed from projected land use and land cover change in isolation (scenario 1). However, the positive effect of warmer ocean temperatures overshadowed the dilution effect, and the population (and its harvest) increased. As modelled, the Dungeness crab population was not sensitive to terrestrial-based changes, largely because those changes did not affect temperature or salinity, which were the drivers in the Dungeness crab production function.

While Dungeness crab and Pacific oyster, as modelled, responded favourably to increases in nitrogen and warmer ocean temperatures, the models did not include several other factors that can affect production and harvest of the two species. An increase in nutrients, especially combined with warmer water temperatures, can lead to low dissolved oxygen conditions, which were not included in the models. Low dissolved oxygen conditions can adversely affect crab and oyster populations (Diaz and Rosenberg, 2008), and the models can be improved by incorporating these damping effects to both populations. Excessive nutrients can also lead to higher turbidity associated with algal blooms, which can affect nearshore habitats such as eelgrass, which are important to Dungeness crab at different periods in their life cycle (Holsman et al., 2006). A decrease in habitat quality or quantity could be included in the model as it affects survival rates throughout the Dungeness crab life cycle. A constant harvest rate was used in both population models. Both models can be improved by including more sophisticated harvest rules. For example, the harvest rate applied to the Dungeness crab population model could reflect changes in demand for Dungeness crab recreational harvest as a function of crab abundance. For Pacific oyster, harvest could be changed to reflect harvest closures that are regularly implemented.
in the Canal when high pulses of freshwater enter the system. These closures are implemented because of the loading of pathogens, indicated by the presence of faecal coliform bacteria, and their uptake by shellfish increases during high freshwater flow events. Additionally, neither species is modelled as part of the foodweb, so any possible unanticipated outcomes as a by-product of foodweb interactions are not included. Finally, our assessment of the impacts of climate change could be expanded beyond increases in precipitation and ocean temperatures to include our best available understanding of how ocean acidification may impact larval survival or other aspects of each species’ life history. For example, changing marine conditions could have non-lethal effects altering such attributes as growth rates, foraging activities, or habitat use. For Dungeness crab, temperature and habitat characteristics of coast estuaries can affect juvenile growth rates with implications for their trophic role and economic value (Holsman et al., 2003).

Ultimately, ecosystems are complex, and it is necessary to (i) simplify the output from ecosystem models or simplify the models themselves to provide management advice and (ii) specify how the scientific advice provided by a model (or modelling system) should be used for resource management. These models can provide heuristic, tactical, or strategic outputs (and associated management advice; Link, 2010).

Heuristic applications include providing basic information on ecosystem functioning, allowing relative importance of different ecosystem processes to be discussed, and generally advancing the understanding of ecosystem and habitat processes. Tactical management applications include suggesting revisions for stock assessments; addressing specific impacts of non-target species, invasive species, and habitat alteration; and allowing managers to consider specific “what-if” scenarios. Strategic applications include: assessing biomass trade-offs (ecosystem-based reference points); evaluating cumulative impacts of non-target species, invasive species, and habitat alteration; and allowing managers to consider general “what-if scenarios” and long-term trends.

Often new models and modelling systems are initially useful for providing heuristic advice. Then through iterative interaction between scientist and managers, models can be revised and improved to provide specific tactical management advice. We envision that the modelling system described in this paper can initially be used for heuristic applications and ultimately for strategic management. The simple models and framework presented here help build intuition about how the system works and also point to specific areas where more detailed models would usefully inform management.

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