

SEA OTTERS, KELP FORESTS, AND ECOSYSTEM SERVICES:  
MODELLING HABITATS, UNCERTAINTIES, AND TRADE-OFFS

by

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## **Abstract**

Resource management is increasingly about the equitable distribution of benefits amongst a diversity of beneficiaries while ensuring the persistence of desirable social and ecological systems. Largely because of the complexity of social-ecological systems, models intended to support integrated resource management continue to suffer from poor treatment of uncertainty, and the challenges of defining appropriate model scope and benefit representation. I explored these challenges through the process of combining field data with population, habitat, and service models to build an integrated model of coastal ecosystem services on the West coast of Vancouver Island, British Columbia, Canada. I examined the trade-offs between sea otter and invertebrate dominated systems under 3 spatial sea otter management plans. The model predicts that an otter-dominated system will produce, in aggregate, between 30 and 90 M\$ / year more than one dominated by invertebrates. Disaggregation by benefits and by location provides insight into trade-offs and equity. For example, the value of increased finfish production from enhanced primary productivity is predicted to be almost double the losses incurred by the invertebrate fishery; while increased detail on the distribution of benefits supports the definition of novel, more equitable and legitimate indicators, allowing management alternatives to be more salient. Development of the model led to advances in the applied and theoretical aspects of integrated model development. Chapter 2 confirms that uncertainties and design assumptions are mostly ignored in the popular modelling literature, and includes a conceptual model to support more consistent model design decisions. In Chapter 3 I characterised key aspects of kelp ecology in Pacific Canadian waters, and showed how the trade-off between precision and accuracy depends on whether one is pursuing knowledge or application. Chapters 4 and 5 tell the story of the integrated model, respectively focusing on ecosystem service production, and the distribution of benefits. My results show how spatial resolution is key to identifying indicators of social and ecological value. All told, my dissertation offers applied, theoretical, and methodological advances in the use of ecosystem models for integrated management. Extending the model to include stakeholder objectives would complete the data-to-decision model, allowing formal decision analysis.

## Preface

The work presented in this dissertation stems from the British Columbia Coastal Ecosystem Services Project (NSERC grant SPG 08-1970). I contributed to the design of this project, and this dissertation represents one its objectives.

Chapter 2 is taken from a pre-copyedited version of Gregr and Chan (2015). Leaps of Faith: How Implicit Assumptions Compromise the Utility of Ecosystem Models for Decision-making. *BioScience* 65(1) 43-54. I was the lead investigator, responsible for concept formation, data collection and analysis, and manuscript composition. Dr. Kai Chan, as the supervisory author, was involved in concept formation and manuscript composition. The manuscript is used here in accordance with the guidelines of the journal. The version of record is available online at: <http://bioscience.oxfordjournals.org/content/65/1/43>.

Chapter 3 has been prepared for submission as a manuscript. I was the lead investigator, responsible for concept formation, data collection and analysis, and manuscript composition. Co-authors include Dr. Daniel Palacios who contributed to the theoretical development and manuscript composition, Ms. Ally Thompson who contributed to the analysis, and Dr. Chan, who assisted with concept formation and manuscript composition.

Chapter 4 has been prepared for submission as a manuscript. I was the lead investigator, responsible for concept formation, data collection and analysis, and manuscript composition. Co-authors include Dr. Villy Christensen who contributed to the concept formation and analysis, Drs. Rebecca Martone and Russel Markel who contributed to the analysis and data collection, and Dr. Chan who was involved in concept formation and manuscript composition.

I expect Chapter 5 to be published as two manuscripts, the first contributing to habitat modelling methods, and the second to the literature on benefits and trade-offs. I was the lead investigator on both topics, responsible for concept formation, data collection and analysis, and manuscript composition. Co-authors will include Ms. Joanne Lessard who

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## **Chapter 1 - Introduction**

The natural world is subject to ever-increasing pressures from a growing human population including resource extraction and habitat degradation. This inter-play between humans and ecosystems, increasingly viewed as a complex, dynamic, social-ecological system (McLeod and Leslie 2009), is critically important to human well-being, not only in economic terms, but also because of social and cultural values (Daily 1997). Ecosystem services (ES) have emerged as a useful lens through which the benefits realised by people can be linked to the ecosystems and species that produce the services from which those benefits are derived (Daily 1997, Granek et al. 2010, Millennium Ecosystem Assessment 2005).

Thus, resource management is increasingly about the equitable distribution of benefits amongst a diversity of beneficiaries while ensuring the persistence of desirable social and ecological systems. This perspective, termed integrated or ecosystem-based management (EBM), has long been recognised as the appropriate approach to the management of natural systems (Grumbine 1994, Slocombe 1998), and contrasts with traditional resource management approaches that focus on maximising yield from a particular resource.

EBM is rooted in the explicit understanding that discrete ecosystem components do not function independently, and that effective management must consider the broader, often indirect, ecosystem-level effects of human activities. Such decisions require an evaluation of trade-offs between alternative management strategies (Levin et al. 2009, Walters 1986), which are perhaps best understood using forecasts of how a range of ecosystem indicators will respond to the different management actions (Levin et al. 2009). Ecosystem models are now widely seen as the way to forecast how such indicators are likely to change in response to various social and ecological drivers (Clark et al. 2001, Pikitch et al. 2004). However, ES analyses continue to rely largely on independent models of ES and ES providers, with little or no interaction between the different components (Norgaard 2010).

The complexity of social-ecological systems makes the development of such models challenging (Oreskes 2003, Walters 1997). Most efforts continue focus either on the spatial or the temporal dimension, but rarely both (Gregg and Chan 2014). An additional challenge is understanding

how to scale local ecological studies to regional scale estimates of ES provisioning relevant to decision making. When considered in combination with the difficulties of representing the uncertainty inherent in models of complex systems, it is perhaps not surprising that despite almost 40 years of effort, the use of ecological forecasts in decision making has been very limited.

The challenges of representing ecosystems in a credible way across space and time, with a reasonable representation of uncertainty, explains in part why one of the most compelling social-ecological problems in coastal ecosystems has been understood only at local scales, and only in terms of its ecology. The recovery of sea otters (*Enhydra lutra*) in Pacific North America has many obvious ecological and social implications. Yet these multiple, regional-scale impacts remain uncharacterised, even while the local scale ecological dynamics have fascinated ecologists for decades.

Using the resource conflict arising from an expanding population of sea otters in coastal British Columbia (BC) as a case study, I address these challenges by developing an integrated ecosystem model to examine how a suite of ES benefits respond to a set of management alternatives. My work spans a range of disciplines and spatial scales, translating local field data into a regional assessment of the benefits under different management scenarios. The empirical work re-enforces the realism of the ecosystem models, while explicit attention to model objectives and assumptions provides useful advances in the treatment and presentation of model uncertainty.

While this work focuses on a marine system, many of the challenges also exist in terrestrial systems, even though the underlying ecological complexity may be less apparent, in part due to slower ecosystem dynamics. Specifically, questions of ecosystem interactions leading to non-marginal change, and the need to better represent and communicate model uncertainty are ubiquitous to models of any social-ecological system. Thus, much of the analysis presented here has implications well beyond the marine environment.

### ***The case study***

On the west coast of Vancouver Island (WCVI, Fig. 1.1), sea otters are re-colonising coastal habitat from which they were extirpated over 100 years ago, thanks to translocation experiments conducted in the 1970s (Nichol et al. 2009). The recovery of this species is seen by many as an ecological success story, as evidenced by their recent downlisting by the Canadian federal government under the Species at Risk Act (DFO 2014). There are, however, those who would disagree.

Sea otters are opportunistic predators that forage on a diversity of coastal invertebrates. During their 100-year absence from the Eastern North Pacific, many of their prey species increased in abundance, allowing humans to develop lucrative fisheries on several including Dungeness crab (*Metacarcinus magister*), geoduck clam (*Panopea generosa*), and sea urchins (*Strongylocentrotus* species). These fisheries are now facing competition from sea otters, and have already been displaced from a number of valued fishing areas (DFO 2014). While this inevitable and on-going fisheries conflict was anticipated almost half a century ago in Alaska (Johnson 1982) and 20 years ago in British Columbia (Watson and Smith 1996), management agencies in Canada continue to struggle with equity issues around the necessary changes to fisheries allocations, which have resulted in economic hardship for certain groups of fishers.

An important aspect of the resource conflict is that the sea otter is understood to be a keystone species (Mills et al. 1993). As sea otters first re-occupy their historic habitat, they prey primarily on sea urchins - an easily accessible prey item (Laidre and Jameson 2006). This releases kelp species from the predation pressure exerted by urchins, and in many cases triggers a trophic cascade {Paine, 1966 #2188}, transforming urchin barrens to kelp forests (Estes and Duggins 1995).

While the effects are subject to considerable spatial and temporal variability, kelp forests are widely believed to lead to higher productivity and diversity of coastal fishes and invertebrates than coastal systems without kelp forests. Three mechanisms for this have been proposed: 1) provision of complex habitat; 2) modification of nearshore currents; and 3) nutritional supplement (reviewed by Markel 2006). Thus, reconciling the sea otter–fisheries conflict is

about much more than the recovery of sea otters and the loss of invertebrate fisheries. It must consider the broader suite of presumed benefits arising from re-established kelp forests.

The benefits of kelp forests (e.g., increases in local primary productivity and reef fish populations) have been and continue to be described in Pacific Canada in some detail through field studies conducted at local scales (Markel and Shurin 2015, Singh et al. 2013, Watson and Estes 2011). However, a critical knowledge gap is understanding how these local observations generalise to a wider geographic region. Filling this gap is important because few management decisions are made at local scales. Instead, they integrate benefits and ecosystem services across more regional extents.

### ***Estimating ecosystem services***

The next step to helping inform regional decision-making is the translation of ecosystem state into ES, the potential benefits that can be realised by people. ES has emerged as an approach for describing, quantifying, and comparing the benefits humans receive from natural systems (Daily 1997, Guerry et al. 2012). The use of this concept has expanded considerably since it featured prominently in the Millennium Ecosystem Assessment of the global effects of ecosystem change on human well-being (Millennium Ecosystem Assessment 2005), and it is viewed by some as the best hope for moving conservation to the mainstream (Costanza and Kubiszewski 2012, Daily et al. 2009).

Application of the ES concept has had considerable success informing and engaging stakeholders and articulating management objectives (Guerry et al. 2012, Ruckelshaus et al. 2015). However, this focus on communication and engagement has left the prevailing tools for operationalising ES research surprisingly light on ecology (Bagstad et al. 2013). Thus, articulating and representing the functional linkages between valued services and the associated service provider is a critical gap in the estimation of ESs. If not addressed, this gap carries the significant risk that stakeholders and decision-makers will be lulled into imagining that complex social-ecological systems are being appropriately represented in available models (Norgaard 2010).

There are 3 distinct barriers preventing the translation of ES knowledge to decision making. Norgaard (2010) argues that a deeper linkage is required between cutting-edge ecological (including social-ecological) research and the needs of decision-makers. Granek et al. (2010) argue for the integrated implementation of realistic models that link the chain of events from management action, through ecosystem change, to ES provision and finally to stakeholder benefits. Others (e.g., Ruckelshaus et al. 2015) emphasise the need to effectively communicate the uncertainty in forecasts of ES benefits.

These challenges are not unique to the field of ES, but are rather part of the larger challenge of characterising and forecasting the state of a complex social-ecological system in response to alternative management actions. This evaluation of indicators under different management alternatives falls squarely in the domain of ecosystem models. These models are myriad, but can broadly be defined as descriptions of how biological ecosystem components respond to different human activities. More realistic versions include some representation of the interactions between the biological and physical components of the ecosystem of interest.

I address these challenges by developing a defensible model of the study system showing how management actions influence the spatial distribution of ES. I illustrate how a vertically integrated ecosystem model allows cutting edge science to be more directly coupled with the needs of decision makers, and allows uncertainty to be more transparently and effectively communicated.

### ***Model uncertainty***

Ecosystem models are fundamental to our understanding of social-ecological systems, and to forecasts of future states. Indeed, models of marine ecosystems are now seen as central to any quantitative EBM effort (Daily et al. 2009, Pikitch et al. 2004). However, there are uncertainties at every step in the process of turning field data into indicators suitable for management. How to characterise and represent these uncertainties in an informative way is the most pressing, challenging, and commonly mentioned gap in both the EBM and the ES literature.

A fundamental source of uncertainty in ecosystem models is the complexity of the system. Well established model design principles (e.g., Jackson et al. 2000, Jakeman et al. 2006, Levins 1966, Loehle 2011, Ord 1979, Silvert 1981) advocate that system complexity be managed by constraining model scope with a clear research question. Indeed, the greatest successes with model forecasts can be observed in resource management contexts (e.g., fisheries management and hydro-electric optimisation) where clear management questions have led to single or fungible sets of well defined indicators that inform well articulated management objectives. This is recognised by approaches like Integrated Ecosystem Assessment (Levin et al. 2009) and structured decision-making (Gregory et al. 2012) which provide the means to clearly characterise the indicators needed for a particular management context.

The need to manage uncertainty in models for management is also recognised in the decision analysis literature (Morgan and Henrion 1992, Phillips 1984). However, the challenge facing ecologists today is that rather than being asked to support specific management objectives or questions, they are increasingly asked rather vague questions about understanding ecosystems. For example the United Nations Environment Program (UNEP), in its introductory guide towards marine and coastal EBM (Agardy et al. 2011), places understanding the ecosystem several steps ahead of choosing management strategies. This focus on understanding is also evident in the peer-reviewed literature. For example Guerry et al. (2012) put the incorporation of ES into policy and management behind knowledge concepts such as understanding resilience.

The response to this quest for understanding has been to increase model complexity, either through the use of coupled models (Parrott 2011, Sutherland and Freckleton 2012, Tallis and Kareiva 2006) where results are passed between largely independent modules (e.g., Daily et al. 2009, Millennium Ecosystem Assessment 2005), or through the expansion of models to include more socio-ecological components and processes (Boyd and Banzhaf 2007, Carpenter et al. 2009, de Groot et al. 2002, Lester et al. 2010). However, there are real limits to model complexity (Arhonditsis and Brett 2004, Costanza and Sklar 1985, Fulton et al. 2003, Silvert 1981, Walters 1997) when modelling inherently open systems that can never be fully specified.

In such cases, increased complexity invariably comes with increased uncertainty (Costanza and Sklar 1985, Fulton et al. 2003, Oreskes 2003). Understanding and representing forecast uncertainty is critical to the use of such models for decision making. Unfortunately, reviews of the literature (Gregg and Chan 2014, Planque et al. 2011) show that uncertainties are rarely considered in ecosystem models.

If the goal is to link science to management and decision-making, placing understanding before the management question is problematic for two reasons. First, models built to "understand the ecosystem" will tend to have vaguely defined scope and lack clear criteria for sufficiency. This is counter to established model design principles and will at best lead to vagueness around model sufficiency and relevance. Without a clear question, there is no way of knowing when a model is adequate. Second, the two goals (understanding vs. forecasting) represent fundamentally different uses of models (Pielke and Conant 2003). Understanding comes from testing hypotheses. Thus, predictions from models intended for understanding are equivalent to hypotheses suitable for empirical testing. Model forecasts tend to be integrative, combining hypotheses that already have some merit. The expectation is that predictions from such forecasting models ought to be subject to very different validation methods (Araujo and Guisan 2006), in part because their validity can never be definitively determined (Oreskes 2003).

Common approaches to model uncertainty include 1) quantification through sensitivity analyses and multi-model approaches; 2) sidestepping by evaluating radically different future scenarios, thereby producing illustrative results of unknown accuracy; and 3) documenting our assumptions and the limits of our understanding (Grimm et al. 2014). Each of these is insufficient in its own way. For example in complex models, quantification is impossible to apply comprehensively, resulting in only a few parameters or model structures being evaluated. Sidestepping is reasonable for illustrative purposes as in broader policy contexts, while explicitly documenting assumptions and limitations is a critical first step, but provides no guidance on integrating, quantifying, and presenting confidence in the overall model.

Given that uncertainties permeate every aspect of ecosystem modelling from data collection to estimates of stakeholder value, asking how much we should believe a model – how credible it is

– requires the entire processing chain to be considered. Note that this is not simply a rollup or cascade of epistemic uncertainties. This would be unfair, since many model components will share assumptions. Rather, it is about a relative assessment of the credibility of all the parts of the model, and an exposition of what are believed to be the least certain parts.

The over-arching theme of this dissertation can thus be characterised as an exploration of ways ecosystem models can be bounded to better support resource management decisions. I use the sea otter case study to illustrate how an integrated approach to ecosystem models, spanning data collection and model development, and benefits estimation, combined with an explicit, comprehensive consideration of uncertainties, can make model results more credible, legitimate, and useful for integrated resource management.

### ***Research questions***

The gap in ecological knowledge related to the ES provided by otter-present vs. otter-absent systems is a potential barrier to effective EBM in this region. Recognising the need for an ecosystem model to fill this gap, my first research question asks how well such models have lived up to expectations with respect to EBM:

*1) Does the treatment of uncertainty in the ecosystem modelling literature provide enough information to assess model credibility?*

The premise being that unless a model's credibility is evident, its utility to managers is severely limited. I investigated this hypothesis with a literature review examining how uncertainty and assumptions are treated in a sample of the most popular published papers on ecosystem models claiming to have management relevance (Chapter 2).

I then turn to the case study and begin my analysis by asking how well can we represent the potential distribution of coastal canopy kelp:

*2) What determines good kelp habitat? How well can we predict it? Is there a difference in the performance of correlative vs. process-based models of habitat suitability?*

The analysis (Chapter 3) illustrates some of the conceptual and methodological challenges of developing a model for understanding the distribution of just a single ecosystem service supply (sensu Tallis et al. 2012). I also use this analysis to emphasise some of the differences between models for understanding versus models for forecasts.

Next, since benefits from ecosystem service providers depend not only on their distribution but also on their abundance, I consider how these abundances may respond to the recovery of sea otters by asking:

*3) What is the difference in ES benefits between otter-present and otter-absent systems on the West Coast of Vancouver Island, BC?*

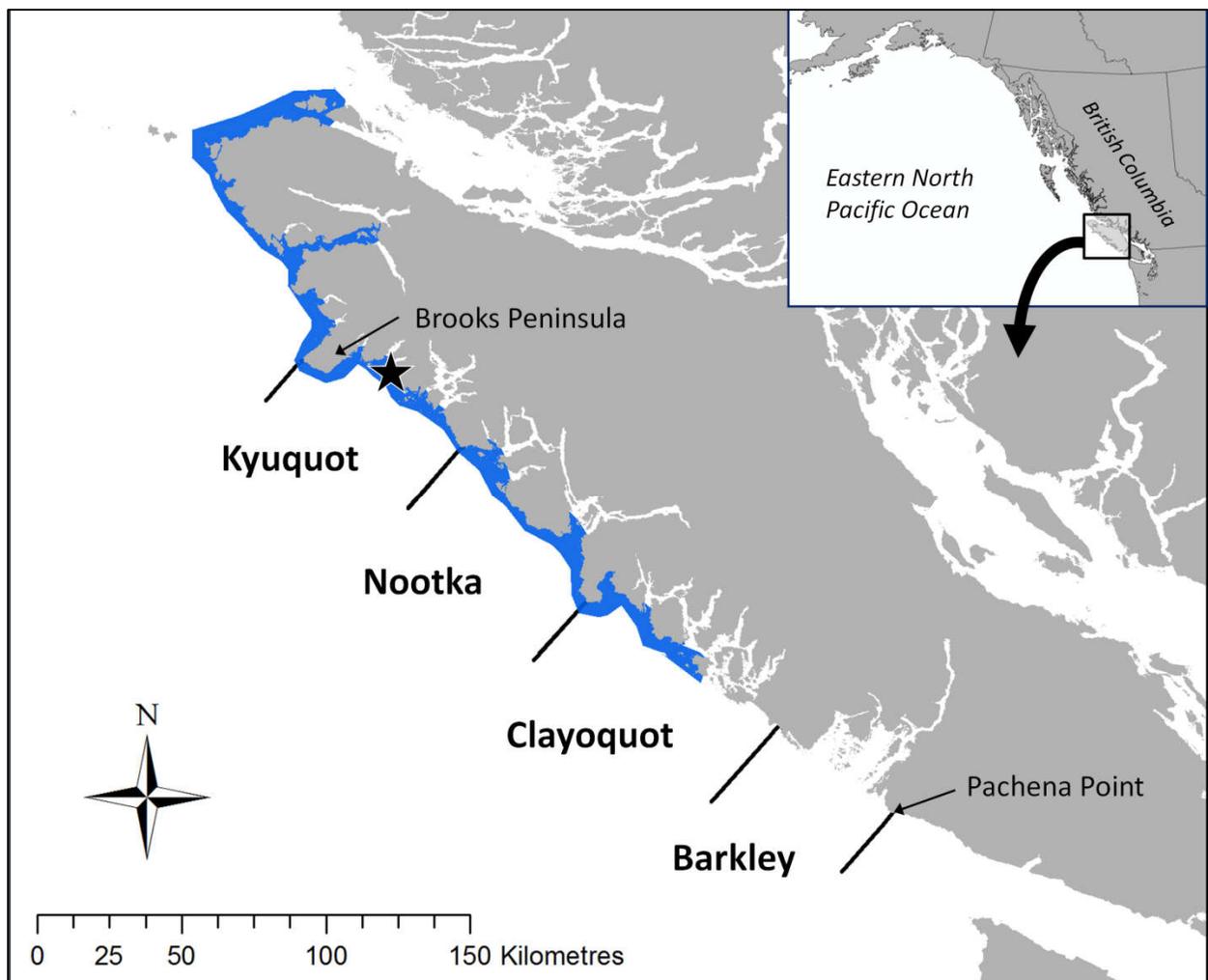
I use an extensive, purpose-collected data set from the WCVI to first create an ecosystem model of the study area without otters. I then model the trophic cascade by re-introducing sea otters into the system and simulating how biomass changes over time for key ecosystem components, and compare the benefits resulting from the two states. I develop a simple benefits model guided by objectives from a structured decision analysis of stakeholder values. I compare the two systems using a suite of 4 ecosystem services (Chapter 4).

Finally, I consider how integrating changes in temporal abundance with spatial distribution can add complexity where it is warranted, in response to a specific management question.

Specifically:

*4) Does understanding the spatial distribution of ES provision influence the ranking of management alternatives?*

To answer this question, I expand the dimensionality of the biomass model in Chapter 4 to include the spatial distribution of valued ES based on the results of Chapter 3. I examine how this additional information allows a broader suite of benefits to be defined, which may influence the ranking of management alternatives (Chapter 5).



*Figure 1.1: The study area on the West Coast Vancouver Island, British Columbia, Canada, showing the area of sea otter re-introduction (black star), approximate current range (blue), and the names of the major sounds mentioned in the text.*

## **Chapter 2 - Leaps of Faith: How implicit assumptions compromise the utility of ecosystem models for decision-making**

Ecological forecasts are increasingly seen as central to integrated management. However, to use such predictions, decision-makers also require some understanding of how likely the forecasts are—or at least how likely one is over another. This cannot be achieved without considering model assumptions and their associated uncertainties. To illustrate, we first reviewed the theoretical aspects of model design and uncertainty, focusing on the role of assumptions. We then examined how the most popular articles on social-ecological models of marine systems reflect these modelling fundamentals. Of the articles reviewed, over half left design assumptions entirely implicit, and 60% effectively ignored uncertainty. This is a fundamental barrier to the use of such models for decision making, and to the broader goal of linking social and ecological models. These consequences, and the suggestions offered to mitigate current faith-based interpretations of ecological forecasts, are salient to anyone creating or using such predictions for decision making.

Predictions from ecosystem models are now widely seen as an appropriate tool for supporting integrated management decisions about social-ecological systems (Curtin and Pallezo 2010, Lubchenco and Sutley 2010). Recent reviews of ecosystem level priorities (Fleishman et al. 2011) and priority research questions for policy (Rudd et al. 2010, Sutherland et al. 2006) have positioned predictions of future ecosystem state as essential to addressing such questions. Indeed, such ecological forecasts are increasingly viewed as an emerging imperative (Clark et al. 2001, Guerry et al. 2012, Sutherland et al. 2006, Tallis and Kareiva 2006).

However, to truly support integrated management (often called Ecosystem-based management, EBM), models must predict a wide range of social-ecological indicators because management alternatives generally impact biophysical, ecological, and social attributes of concern. The recognition that EBM is inherently place-based (McLeod and Leslie 2009) further requires such temporal predictions to include a spatial component. The necessity to span social-ecological, temporal and spatial dimensions is unique in the history of modelling.

While the utility of such predictions for choosing among alternative futures is self-evident, it should be equally clear that point estimates (e.g., Millenium Ecosystem Assessment 2005) do not reflect the uncertainties inherent in the modeled systems. Evidence from cognitive science suggests people are overly swayed by what they are presented, even if they know there is missing information (Kahneman 2011). Thus, decision-makers may treat point estimates as if they were essentially true unless uncertainties are presented alongside such predictions. The widespread absence of such a juxtaposition puts both decision-makers and scientists in vulnerable positions: decision-makers cannot appropriately evaluate the risks associated with uncertainty, while scientists are open to criticism of their methods, accusations of bias, and loss of credibility.

If model predictions are used to compare trade-offs between alternative futures, decision makers need to understand not just what is being predicted, but also how likely it is compared to the alternatives. A comprehensive - and comprehensible - presentation of the uncertainties underlying model output is therefore a necessary first step towards effective use of such predictions in decision making.

Unfortunately, the comprehensive treatment of uncertainty is confounded by the assumptions used to reduce the complexity of the study system to make models tractable. Modellers, oriented by a clear question (Jakeman et al. 2006, Levins 1966, Müller et al. 2011, Ord 1979, Silvert 1981), use assumptions to decide what to include and what to omit. The omitted parts generally become externalities - entities or processes assumed to have negligible influence on model results. While such reductionism is critical to advancing our understanding, it is fundamentally at odds with the holistic needs of integrated management. Being explicit about assumptions, and our belief in them, is thus essential to both the characterisation of uncertainty and to the uptake of model results by decision makers.

Given this purpose-built nature, models are naturally used in a variety of ways. Projections (models of future state based on particular assumptions) are often developed to advance our understanding, allowing testing or comparison of different hypotheses, while forecasts strive to more precisely predict what *will* happen, not just what may under stated conditions. While the

objectives and precision of such predictions will differ, their interpretation in all cases depends on the confidence we have in the models. Thus, the need to be explicit applies to all model predictions, regardless of purpose.

The consequences of implicit assumptions and uncharacterised model uncertainty are significant to both science and decision-making. For scientists, leaving assumptions and uncertainties implicit makes our work incomplete, thereby magnifying dramatic failures (e.g., He and Hubbell 2011) and casting doubt on our ability to predict ecosystem response to management actions (e.g., Robinson and Frid 2003, Schneider and Kuntz-Duriseti 2002). For decision makers, there is risk in the uncertainty behind every assumption. Implicit assumptions therefore hide the risk of using ecosystem models to inform decisions. Given that model uncertainty has led to failures in resource management (Ludwig et al. 1993), many decision makers choose to rely instead on established practices and expert judgment (Cook et al. 2009, Pullin et al. 2004). At worst, difficult but important decisions can be delayed (Maslin and Austin 2012, Rose and Cowan 2003), or model uncertainty can be used to legitimise decisions rather than guide them (Robinson 1992).

Without an explicit consideration of model assumptions and their underlying uncertainties, decision makers and inter-disciplinary researchers are unable to assess the risks such (often discipline-specific) assumptions may entail. Fully integrating model results into decision making will require a broader effort to more appropriately deal with the management of uncertainty, a fundamental aspect of what has been described as post-normal science (e.g., Funtowicz and Ravetz 1994). Characterising the relationship between model assumptions and uncertainty represents a critical first step in that effort.

Given such potentially significant consequences, how do models intended to inform EBM actually treat the assumptions and uncertainties inherent in social-ecological systems? Are uncertainties comprehensively represented as they accumulate in different parts of the model? Is the uncertainty in model design assumptions evaluated, or at least considered in terms of possible impact on model outputs? In the absence of any such assessment, it is virtually impossible to gauge the value of model predictions to decision-making.

To answer these questions, we first consider the role of assumptions in model design, and characterise their relationship with model uncertainty. We then explore how these design assumptions and their associated uncertainties were treated in a sample of the most frequently cited articles describing marine EBM models over the last 22 years. We examine how different disciplines treat assumptions and uncertainty, and conclude with recommendations about how assumptions and uncertainty in ecosystem models could be more explicitly characterised, and the benefits we expect would accrue.

### ***Theoretical framework***

The role of assumptions is acknowledged in the extensive literature on model design, and the need for a clear statement of assumptions and their implications is often emphasised. However, unlike parametric statistics, where necessary assumptions are widely documented, there is no widely accepted categorisation of the types of assumptions needed for social-ecological models. Such a typology is necessary to describe the degree to which fundamental model assumptions are either stated or left implicit. We therefore begin by creating such a typology, identifying the types of assumptions necessary for each of four distinct model design decisions: extent, resolution, process representation, and data use.

The importance of starting with a clear model objective is emphasised repeatedly in the literature (e.g., Jackson et al. 2000, Jakeman et al. 2006, Loehle 2011, Ord 1979, Silvert 1981), and is fundamental to the design process. We argue that this objective must be sufficiently detailed to clearly inform decisions about model extents and resolution, leading to the first set of model assumptions. This definition of model scope (extents and resolution) is the first step in model design, and constrains subsequent design decisions about process and data use.

Model extents define the boundaries of the modeled system, which can be distinguished with three axes – Time, Space, and Richness (Fig. 2.1). Along the temporal axis, models vary from single, static snapshots to population dynamic models where contemporary work focuses on predator-prey dynamics (e.g., harvest) and population response to a changing climate. On the spatial axis, models vary from the aspatial (which assume homogenous mixing) to the biogeographical - how species are distributed in space, which underpin studies of critical

habitat, marine protected areas, and spatial planning. The complex dynamics on each of these axes historically led researchers to explicitly represent variation in either the temporal (e.g., population dynamics) or spatial (e.g., biogeography) dimensions - a distinction that largely continues to define the fields today. The third axis, which we call Richness, is defined broadly as the breadth of social, biological and/or physical components selected from the social-ecological system of interest, recognising that a fundamental division exists between biotic (e.g., individuals, populations, functional groups) and abiotic (e.g., habitat indices or climate forces) components. Richness thus defines the components of the system to be modeled across space and/or time. For example, the richness extents of a single-species population model may include prey or predator species, competitors, and perhaps one or more physical variables such as temperature. For management models of commercial species, this richness would typically be extended to include harvesters, and often market components (e.g., landed value, fuel and gear costs). Importantly, anything not explicitly included in a model's extent becomes an externality, and represents the first of many (often implicit) assumptions modellers must make.

The model objective also informs the choice of resolution across each axis, with this choice constrained by the selected model extents (particularly Richness). Temporal e.g., (time-steps, seasonality) and spatial (e.g., grid-cell size, survey density) resolution are relatively intuitive; resolution on the richness axis specifies to what detail the selected components are described. In richer models, the dynamics can become extremely complex, typically necessitating reductions in resolution on one or both of the other two axes.

Within this defined model scope, we then move to defining model structure: the relationships between model components. Defining model structure is typically guided by general principles or hypotheses about system function. Decisions are needed about which relationships (processes) to include, and how they will be represented (data use).

Decisions made at each step in the design process (extents, resolution, process, data) have associated assumptions which together form a logical hierarchy, where each design decision is constrained by the assumptions and decisions from the previous steps, even when models are

iteratively designed. While every model will differ in detail, we have identified some general features of the assumptions made at each stage of the design process.

For example, choosing model extents assumes that whatever is left external to the model (whether space, time, or components) will either not notably influence the model results for the question at hand, or is not well enough understood to be included. Similarly, decisions about resolution restrict the types of possible interactions between the chosen model components (e.g., individual organisms, species, or populations), creating the potential for process externalities.

Explicit processes (i.e., those included in the model) require assumptions about how the relevant components interact, and how they are distributed in time (Fig. 2.1b) or space (Fig. 2.1f). Process assumptions are often implied by the type of model structure selected. For example simple regression and many correlation analyses assume linear relationships, while off-the-shelf tools (e.g., Bagstad et al. 2013) all impose certain structures, each with their own assumptions about process.

Assumptions are also made about data. Ecosystem models can be described as an assemblage of available data and hypotheses. Since data are rarely collected specifically for a particular ecosystem model, the relevance of the data used is pertinent. Assumptions relate to the degree of independence or bias attributed to the data, and their suitability for model parameterisation or evaluation. Assumptions about parameters and data also depend on model structure. For example, statistical models used to estimate parameters from data have assumptions about model structure and data suitability (e.g., independence, unbiased sampling). Other aspects of representativity (e.g., how transferable the life history data are across time, or space) may also be relevant.

We propose that the collection of assumptions described here – required by all models of social-ecological systems - can be organised into a generic typology that parallels the steps in the design process. This typology includes assumptions about externalities, component complexity, process relevance, component-component interactions, component dynamics,

stationarity (the assumption that parameters are constant over time or space), and data relevance (Table 2.1).

We recognise that these aspects of model design (i.e., model scope, selection, specification, and data suitability) are commonly dealt with in the literature. However, the typology we describe unifies these concepts within the challenges of overall model design, illustrating the consequences of assumptions at different steps. We believe that this perspective will provide guidance, particularly to decision makers and novice modellers, about the relationship between design decisions, assumptions, and associated uncertainties, in a way that is difficult to appreciate from individual model design steps. By articulating the relationships between model assumptions and uncertainty, our typology complements previous efforts (e.g., Grimm et al. 2014, Grimm et al. 2010) to standardise how the rationale, design, and testing of ecosystem models is documented.

### ***Model uncertainty***

Although uncertainty has been characterised in various ways (e.g., Mangel 2008, Morgan and Henrion 1992, Regan et al. 2002), the contribution from model assumptions appears to have not been considered in any detail. We found that assumptions relate primarily to three types of epistemic uncertainty: structural (roughly, how the system works), parametric (how the interactions between components are quantified), and observational (how we measure and interpret what we see). While not independent, each can be associated with specific aspects of model design (Table 2.1) and thus to the different types of model assumptions.

Structural uncertainty is related to model extents, resolution, and process and is also influenced by unknown or excluded processes or relationships (i.e., unrepresented, confounding variables). Because of its pervasiveness, structural uncertainty is believed to dominate parametric uncertainty, particularly in biological systems (Wood and Thomas 1999). Processes can be as simple as the choice between a linear or non-linear relationship between response and predictor variables in a regression model, or it can be as complex as representing the evolving social values resulting from multiple actors interacting in a dynamic environment.

Parameter uncertainty relates to the quantification of model processes. This is typically done by fitting assumed relationships using available data, or taking established parameters (e.g., on population growth rates) from the literature. Parametric uncertainty comes from the variability in such empirically specified parameters, and from unknown or mis-specified parameters. The potential for parameter mis-specification stems from the synthetic nature of ecosystem modelling, where modellers must often make do with what can be observed, while recognising such data may not be entirely suited to the task (e.g., Pauly et al. 2013). The common assumption of stationarity also tends to produce parametric uncertainty, since few parameters are constant over space and time.

Observational uncertainties relate to data quality and include sampling error and bias. Ecologists are taught to understand observational uncertainty from the perspective of field studies, where concern about replicates, controls, and other aspects of experimental design are manifest. Unfortunately, designed ecosystem-level manipulations are very difficult to conduct. Accordingly, using data collected under one set of conditions necessarily entails uncertainty when used to parameterise a model for different conditions. Similarly, neglecting such uncertainties during model validation can lead to overly optimistic assessments of model performance.

We recognise that uncertainty is commonly addressed by comparing models to data, and that such empirical tests are essential to understanding model performance. However, the ever-increasing complexity of ecosystem models means we have neither the data nor the methods to test them thoroughly (Fulton et al. 2011). Thus, as ensemble approaches and other holistic evaluation methods are developed it becomes even more critical that we be explicit about assumptions and the degree of confidence we have in them.

### ***Review methods***

To obtain a sample of the literature for analysis, we applied a series of hierarchical searches to capture a representative sample of the published literature on marine ecosystem models claiming management relevance. We analysed the collected articles to characterise the degree of disciplinary in the ecosystem modelling literature (as might be expected given that model

scoping decisions are made across the 3 different axes - Fig. 2.1), and to assess how assumptions and uncertainties were represented in the 60 papers with the highest citation rates.

We searched 3 databases (Web of Science, BIOSIS, and Zoological Record) for the years 1990 to 2012 using 3 sets of key words. In all cases we searched the "Topic" field and combined all keywords using the AND operator, except as noted. Only articles that described a model (or models) purported to inform management were assessed. Review, framework, methods, and theoretical articles were not considered.

Our first ('ecosystem') search used the key words "marine", "ecosystem model" and "management". We assumed this would capture the literature on ecosystem modelling for decision-making in the broadest – but not necessarily the most exhaustive – way.

In the second ('habitat') search we replaced "ecosystem model" with ("habitat model" OR "habitat suitability") and "management" with ("management" OR "conservation"). These refinements were intended to examine whether habitat models were seen as distinct from ecosystem models. The first substitution included two terms because both are commonly used to describe spatially explicit models. The second substitution reflects our observation that such models are often seen as specifically relevant to conservation.

With the third ('social-economic') search, our intent was to isolate modelling efforts that explicitly included social or economic considerations. The search terms included: "marine", ("ecosystem" OR "habitat"), "model", ("social" OR "economic"), and "management".

We evaluated our hypothesis of disciplinary fragmentation by examining the overlap between the different search results, and by searching within each group for keywords from the other two groups. We then ranked the papers according to their annual citation rate, and selected the 20 highest ranking papers from each search for a more detailed assessment, thereby selecting the articles with the highest impact on the modelling field (based on number of citations per year).

In the detailed assessment we first examined the stated objectives for each paper, allowing for multiple objectives if stated explicitly. We grouped objectives into 5 classes, defined to further test our hypothesis that different disciplines (and hence literatures) are located in different parts of the model scoping space (Fig. 2.1). Objective classes included 1) Representation; 2) Hypothesis testing; and predictions across 3) Space, 4) Time or 5) Richness.

We then explored how assumptions were treated in our sample of the literature, noting for each article how well it articulated assumptions for each phase in the model design process (Table 2.1). Using an ordinal scale, we recorded whether *any* assumptions were mentioned when discussing model design, model interpretation, both, or not at all (Table 2.2). We applied very lenient criteria, requiring only a single explicit assumption for a paper to score a mention (ecosystem models must make numerous assumptions at each design phase). Each paper was given a single score for each design phase (Extents, Resolution, Process, Data). We used a similar approach to score how uncertainty was articulated. Our ordinal scale recorded whether *any* treatment of uncertainty was conducted, or whether uncertainty was mentioned in the design or interpretation of the model, mentioned in passing, or not at all (Table 2.2). Again, to be lenient, we required only a single explicit statement of uncertainty for an article to record a mention.

## ***Results and discussion***

### **Disciplinary fragmentation**

There was obvious fragmentation of the ecosystem modelling literature across ecological interactions, habitat considerations, and social-economic implications. Of 560 papers found, only 21 (< 5%) appeared in more than one search, and only a single paper was common across all three searches, emphasising the relative isolation of these 3 modelling sectors (Fig. 2.2).

Assuming the number of journals provides a coarse indication of topic diversity, the 253 'social-economic' articles displayed the greatest diversity with papers in 104 journals treating topics ranging from marine reserve design to carrying capacity, eutrophication, and ecosystem service valuation. In contrast, the 160 articles identified from the 'ecosystem' literature, spread over 69 journals, was dominated by population and trophic models, and included a handful of biological

oceanographic models. The 'habitat' search yielded 140 articles in 76 journals, with the majority focused on habitat suitability for particular species, with a small number focused on physical classification.

The separation of the ecosystem and habitat literature is further illustrated by the lack of cross-referencing. We found the word "habitat" in only 12% of the 'ecosystem' abstracts, while "ecosystem" occurred in only 19% of the 'habitat' articles. In contrast, over half (61%) of the 'social-economic' article abstracts included the word "ecosystem", and 32% contained the word "habitat". This is understandable since habitat or ecosystem models generally underpinned the social-economic analyses. However, while the 'ecosystem' and 'habitat' article abstracts contained the fragment "soci" or "econ" in roughly the same proportion (34% and 27% respectively), the social-economic analyses presented in these cases were very limited in scope, often limited to monetary valuation of a small number of ecosystem components. This suggests that the social-economic language was used in these cases primarily to valorise the articles - that is to burnish their apparent social-economic relevance.

The vast majority of papers (54/60) had *prediction* of one kind or another as their primary purpose (Fig. 2.3), without explicitly using these predictions to test hypotheses. Of the remaining papers, 4 declared *representation* to be their fundamental objective, and 2 (ecosystem models) explicitly stated *hypotheses for testing*. Whether predictions were across space, time, or richness varied across model type (Fig. 2.3a), with almost half (26/60) reporting predictions along more than one scoping axis, mainly combining space and time (Fig. 2.3b). Over half of the ecosystem models also included habitat, while habitat papers focused almost exclusively on spatial predictions. The social-economic papers showed the greatest diversity of objectives, and virtually all had clearly stated management relevance.

These lines of evidence lend strong support to our hypothesis of disciplinary fragmentation across our proposed scoping axes. The uniqueness of the search results confirms our selected keywords reflect unique jargon emerging from the three different modelling sectors. The rationale for this is evident in the complexity each must deal with on its primary axis of interest. For example, ecosystem models that included habitat used spatial box models of relatively poor

resolution, in some cases considering only 2 boxes, whereas habitat models generally produce spatial predictions on relatively high-resolution grids. Such fragmentation is thus understandable largely unproblematic, though difficulties are likely to arise when coupling models across sectors if assumptions are not treated comprehensively and appropriately.

### **Reporting of assumptions**

When the four design phases we defined (extents, resolution, process, and data) are considered in aggregate, over half of the necessary assumptions were omitted by the 60 articles reviewed (Fig. 2.4). Assumptions about data were most commonly overlooked, while assumptions about process were most commonly articulated (Fig. 2.5). In terms of model sectors, 'ecosystem' articles left all assumptions implicit 39% of the time, while 'social-economic' papers articulated no assumptions 68% of the time (Fig. 2.4). Only 3 articles articulated one or more assumptions in each of the four design phases, while five made no mention of assumptions at all. When explicit, assumptions were most commonly mentioned in the methods; appearing in the interpretation sections about half as frequently. Within any individual paper, assumptions (not necessarily the same ones) were mentioned in both the methods and interpretation sections less than 25% of the time, and never by a social-economic article.

While we recognise the difficulties associated with publishing extensive model detail (see below), the ad hoc treatment of foundational assumptions in the articles we reviewed should give the reader pause. The social-economic models made *no mention* of assumptions over two-thirds of the time, and only 15% mentioned assumptions during model interpretation. Cumulatively, the most fundamental assumptions about model extents were not mentioned almost half the time, while those dealing with the more complex situation of data suitability were overlooked most often (over 70% of the time). Even many of the papers scoring well (i.e., 'both') in our assessment left many assumptions implicit, because our lenient criteria for scoring a mention required only a single assumption to be articulated. While these concerns do not apply to all ecosystem models, they do seem to apply to the most frequently cited ones. This likely hampers the uptake of model results by decision makers and makes it more difficult

for those hoping to improve model relevance by coupling ecological and social models (e.g., Kareiva et al. 2011, Parrott 2011, Sutherland and Freckleton 2012).

Despite differences in how implicitly the three sectors treated assumptions within the four classes of design decisions (Fig. 2.5), the relative prominence of process-related assumptions (e.g., almost all of 'ecosystem' articles mentioned some aspect of process in either the methods, interpretation or both) illustrates the importance of model dynamics. However, since processes are tied to model scope (extent and resolution), model results can only be understood and interpreted within that defined context (e.g., a model that predicts a species' annual biomass cannot reasonably inform a monthly catch limit). Thus, leaving out the underlying scoping assumptions provides insufficient context for interpreting results, at considerable risk to those using the model outputs. This most clearly manifests in the social-economic analyses, which, while clearly dependent on some kind of underlying spatio-temporal ecological analysis, articulate notably fewer assumptions than the technical models themselves. With so many assumptions implicit, such models leave much to faith, thereby significantly reducing the value of the information they provide.

### **Model uncertainty**

As with model assumptions, most of the papers reviewed (60%) either made no mention of uncertainty or mentioned it in passing (Fig. 2.6a). Perhaps most importantly, only 10% explicitly discussed the role of uncertainty in the interpretation of results, leaving 90% of the papers reviewed without the information necessary to evaluate model accuracy. This aligns with earlier work regarding model purpose by Robinson and Frid (2003) and Seppelt et al. (2011) who found a large number of articles describing model results that could not be evaluated for their stated purposes because of poor documentation. It is remarkable that despite a ubiquitous understanding that uncertainty exists, and a peer-review principle of reproducibility, many published articles contain only point estimates (implying unequivocal validity), and an insufficient description of how they were produced. How did we get to this point?

We suggest that the current trajectory of implicit model development is rooted in the incompatibility between the inherent complexity of social-ecological systems and the focus of

scientific publishing on concise, interesting results. Authors' and publishers' twin goals of growth in readership and numbers of publications likely lead towards stricter page limits and a preference for punchy conclusions. Since models are often a complex amalgam of laws, theories, assumptions, and data (Oreskes 2000), a detailed description of model design decisions is unlikely to be either brief or punchy. Thus, unless such rigor is demanded by editors or reviewers, many published articles describing ecosystem models are likely to continue failing the repeatability test.

The emphasis on interesting findings also means that the presentation and discussion of model uncertainties is not a strong recipe for acceptance. In fact, technical articles seem to receive reduced readership (Fawcett and Higginson 2012), which likely contributes to our finding that popular articles contain limited technical detail. Nevertheless, the resulting feedback loop, where notable results are increasingly prioritised over model rigor and repeatability, reinforces the obfuscation of assumptions and their associated uncertainties. The problem is likely compounded when authors presume their primary audience is comprised of like-minded researchers, who might normally make similar assumptions. The result is increasingly isolated modelling communities, where more and more assumptions are hidden, thereby obstructing model integration across sectors.

A second cause of overlooking key assumptions is technical, a function of the reductionist approach traditionally used to understand portions of the system. As we have described, every modelling exercise requires scoping assumptions to 'remove' much of the system uncertainty and make the model tractable. This makes it more likely that the analysis may uncover how some small portion of the system functions. However, since such analyses are typically embedded in the institutionalised insularity described above, the scoping assumptions and the uncertainty they obfuscate are rarely revisited, even though they are critical to understanding the model and its implications for science communication and decision-making.

This leads to the challenge of evaluating ecosystem models. Of the 17 articles presenting some form of empirical validation, 14 applied sensitivity analyses, and there were individual examples of ensemble forecasting, qualitative analysis, and model averaging. The sensitivity analyses

generally involved varying fewer than 5 parameters, usually across a small number of fixed values. The other methods applied examine holistic model performance. Validation is thus either partial, or integrative, telling us little about what parts of the model are the most uncertain (though more comprehensive sensitivity analyses can be done within specific domains, e.g., Gibson and Spitz 2011). Given that the complexity of ecosystem models will continue to present a significant challenge to whole system testing for some time (Fulton et al. 2011), it is imperative that untested or disciplinary-specific assumptions be made explicit and their implications considered.

Not dealing explicitly with model assumptions and uncertainty in model outputs will be increasingly problematic as models move towards the valuation of ecosystem services (Bockstael et al. 2000), an approach now broadly adopted to relate natural capital to economic, social, and ecological values with the hope of bringing conservation into the mainstream (Daily et al. 2009). Such valuations clearly depend on the underlying models of social-ecological function (Kareiva et al. 2011). Thus, the obfuscation of uncertainty through implicit assumptions does not bode well for improving our understanding of how ecosystem services are produced and valued. This is particularly salient as researchers begin bringing non-monetary values into ecosystem service assessments (e.g., Chan et al. 2012, Daniel et al. 2012), where explicit treatment of assumptions and uncertainties will be even more crucial given the context-dependence of such values (Russell et al. 2013, Satterfield et al. 2013).

Increasing model complexity while focusing on point estimates has also led to the increasingly common view that models of ecosystem services will be improved with additional data (e.g., Lester et al. 2010) or by increasing complexity either through the coupling of ecological and social-ecological models (e.g., Lester et al. 2010, Parrott 2011, Sutherland 2006, Tallis and Kareiva 2006) or greatly expanding model extents (e.g., Purves et al. 2013). However, there is no evidence increased model complexity improves model performance; rather, models seem to perform best with intermediate complexity (Costanza and Sklar 1985, deYoung et al. 2004, Fulton et al. 2003, Hannah et al. 2010). Increased complexity is also likely to increase model uncertainty through the addition of 'known unknowns' (Maslin and Austin 2012), as will filling

data gaps that elucidate previously hidden or unknown complexities. While such efforts may improve our understanding, they should also reduce the confidence we place in the model predictions.

In addition to a common tendency to overlook uncertainty, we found notable differences in how the three modelling sectors treated uncertainty. Habitat modelling articles were the least forthcoming, while ecosystem articles were the most likely to discuss uncertainty in their interpretation of model results (Fig. 2.6b). We suggest this reflects the relative maturity of these two fields: ecosystem models are based on well-established population dynamics, thus lending themselves more to interpretation, while habitat models continue to be largely explanatory, without clear hypotheses about spatial dynamics, making discussions of the role of uncertainty somewhat premature. Finally, social-ecological articles were the most likely to apply some sort of uncertainty treatment (Fig. 2.6c). And while this continues to be largely focused on parameter uncertainty (and hence sensitivity analysis), it at least shows an appreciation for the role of uncertainty in decision-making. Importantly, we found no explicit discussion of uncertainties related to stationarity, although authors often conceded that many ecological processes do not remain constant from year to year.

We must emphasise that because our review focused on popular articles, it may be indicative of norms, but not the cross-section of practice across the modelling community. On the contrary, dealing with uncertainty is an active and growing area of research. However, such articles are necessarily somewhat technical and such articles are less popular on average (based on citation rate - Fawcett and Higginson 2012). While it is likely that the technical literature is being read by, and influencing experienced modellers, there is scant evidence of its application to management in the popular articles we reviewed. Thus, it would appear that important work on uncertainty is not being communicated between disciplines or across the science-policy interface, potentially leading to the acceptance (or rejection) of model results based largely on faith.

## ***Recommendations***

Comprehensive scenario analyses rather than ad hoc sensitivity analysis, multi-model inference, and bounded parameterisations are currently the most effective means of handling uncertainty in models for EBM (Fulton et al. 2011) and best practices are emerging (Link et al. 2012). While such methods will undoubtedly improve our confidence in the explanatory power of such models, any treatment of uncertainty relevant to decision-makers must also expose and characterise model assumptions. We therefore, first and foremost, encourage modellers to adopt (and journal editors to require) an explicit discussion of critical design assumptions – and the possible consequences of their violation - as standard modelling practice. Characterising model limitations in this way – even qualitatively – is, we believe, the first step in providing decision makers and other modellers with a more explicit understanding of, and consequently more appropriate expectations about, the confidence to be placed in model output.

Assumptions about model extent and resolution are perhaps the easiest to articulate, and given our observation that they define model externalities and constrain subsequent model design, it is worth articulating how relevant the externalities may or may not be to decision makers. We also recommend emphasising model structure, since very small changes in structure can lead to dramatic differences in prediction (Wood and Thomas 1999). Being explicit about model structure and parameterisation will ensure conclusions are as transparent as possible (Schneider and Kuntz-Duriseti 2002). Multi-model approaches, originally advocated by Levins (1966) who insightfully remarked that "truth is the intersection of independent lies", currently provide the most useful way of treating such structural uncertainty (Fulton et al. 2011, Link et al. 2012).

One of the most surprising results from our review was the widespread faith in data quality and suitability. We found that data were, by and large, assumed to be representative and accurate (a version of Kahneman's "What you see is all there is" problem). We see this as particularly problematic for ecosystem models where a diversity of existing data sets, collected for different purposes, are typically combined and used for both parameterisation and to describe initial conditions (in simulation models). Although scenario analyses (i.e., the examination of how

model performance responds to different parameter sets, processes, or model structures) can deal reasonably well with parameter uncertainty, data used to specify initial conditions often has a greater influence on model predictions (Fulton et al. 2003, Hannah et al. 2010, Langford et al. 2009). Understanding how sensitive model predictions are to parameterisation and initial conditions is therefore critical to model robustness.

A consistent, on-going effort to articulate model assumptions may advance our understanding of how assumptions can be categorised, ultimately leading to practical guidelines about which assumptions are most suitable for different objectives, scope, and complexity. Our proposed assumption hierarchy organised around model design phases provides a discipline-independent approach to begin organising this information, and allows design assumptions and their associated uncertainties to be treated in a more structured and consistent manner. Further, since the detailed documentation envisioned here and advocated by Grimm et al. (2010) is likely to remain unsuitable in primary publications, we encourage authors to make such technical details available either as supplemental material or as literature citations. Ideally, such reports would eventually become required companion documents to articles on ecosystem models. We are far from the first to emphasise that computer models cannot replicate complex systems. Every model must make unavoidable trade-offs between generality, accuracy, and precision (Levins 1966). Thus, our models may be much better received, and the results much better communicated, if these trade-offs and associated simplifying assumptions are described and explicitly related to the fundamental model objectives. For example, model design often begins with a fundamental trade-off between tactical (short-term) or strategic (medium to long term) objectives (Christensen and Walters 2005). This and other scoping decisions rest upon the question the model is intended to answer. Thus, a clear, well-articulated question allows us to develop model complexity where necessary (deYoung et al. 2004), and to carefully manage the trade-off between the number of model components and their detail (i.e., richness vs. resolution) (Hannah et al. 2010).

## ***Conclusions***

Our review of the most widely cited marine ecosystem modelling literature of the last 22 years illustrates how popular articles largely leave most model assumptions implicit and treat uncertainty very unevenly, often omitting it in the interpretation of model results altogether. Thus, despite claim of management relevance, the papers reviewed generally provided very little information with which managers and policy makers could evaluate the risks associated with the uncertainty in the model predictions. While this is by no means ubiquitous, having the most widely cited articles being those with most model assumptions and uncertainties implicit has significant consequences for the development of any integrated models of social-ecological systems, and has profound implications on how decision-makers treat the outputs from such models.

Without explicitly considering scoping assumptions across the temporal, spatial, and social-ecological axes described here, model coupling efforts are more likely to simply assume suitability of the component models. This potential for model mis-application may be magnified if, as we propose, assumptions at each of the four stages of model design hierarchically constrain design decisions at subsequent stages. More exchange among modellers from different disciplines might lead to a greater emphasis on unearthing implicit assumptions and a fuller characterisation of the resulting uncertainties. Until model assumptions and related uncertainties are articulated in a more explicit, preferably standardised way, the hope that complex, integrated social-ecological models will appropriately evaluate the impacts of management actions seems misplaced. Without the guidance that such an explicit treatment provides, complex models of social-ecological systems will continue to run the very real risk of being inappropriately used.

Leaving assumptions implicit and ignoring uncertainties may be pragmatic in the short-term, but it hinders the ability of others to understand the limits of our models. More critically, ignoring uncertainty is reckless because as a fundamental component of risk, its omission leaves a critical gap in evidence-based decision making. Models with implicit assumptions and hidden uncertainties do not constitute evidence. If we hope to support decision-makers with

forecasts based on what we know, we must pay equal attention to *how well we know it*, and *what we don't know*. At a minimum, we must be better at articulating our model assumptions, and when appropriate, we should strive to communicate our model results in probabilistic terms based on known uncertainties rather point estimates. In this way, model predictions could be integrated into decision making tools and coupled models without asking (or allowing) scientists and decision makers to make blind leaps of faith.

*Table 2.1: Typology of typical assumptions made during model design and the phase to which they belong, the main type of uncertainty associated with them, with examples.*

<b>Assumption type</b>	<b>Design phase</b>	<b>Uncertainty</b>	<b>Examples of common assumptions</b>
Externalities	Extent	Structural	The model scope is sufficient. Life history is the main determinant of long term population size. The selected model components are sufficient to represent key processes and indicators.
Actor complexity	Resolution	Structural	The selected actors are sufficiently disaggregated to represent both the interactions of interest, and those that dominate the system. Groups of actors will all have identical dynamics and interactions.
Process relevance	Resolution	Structural	Unrepresented processes are constant, or their effects average out. The processes of interest operate at the selected spatio-temporal resolution.
Actor interactions	Process	Structural Parametric	Actors with no interactions operate independently in the model. Modeled interactions sufficiently capture processes of interest.
Actor dynamics	Process	Structural Parametric	Representation of space and time sufficient to represent drivers of interest. Dynamics are appropriately represented and parameterised.
Stationarity	Process	Structural Parametric	Space (i.e., habitat) has no significant effect on life history parameters (e.g., Fig. 2.1 a, b, e). Modeled actors are uniformly distributed in space. Temporal dynamics are at equilibrium (Fig. 2.1 c, e, f).
Data relevance	Data	Observational	Collected data are representative of the population of interest. Data are unbiased.

*Table 2.2: Review criteria and ordinal levels used to describe how uncertainty and assumptions were handled by ecosystem models appearing in the scientific literature.*

<b>Category</b>	<b>Description</b>	<b>Level</b>	<b>Description</b>
Assumptions	To what degree were assumptions described at each of the 4 levels?	None	No mention of assumptions
Extent		Interp	Mentioned in model interpretation
Resolution		Methods	Mentioned in model methods
Process		Both	Mentioned in both methods & interpretation
Data			
Uncertainty	To what degree was uncertainty mentioned or addressed?	None	No mention of uncertainty
		Mention	Mentioned in passing with no consequence
		Interp	Mentioned and influenced interpretation
		Methods	Mentioned in methods and influenced design
		Treatment	Some aspect of uncertainty explicitly treated

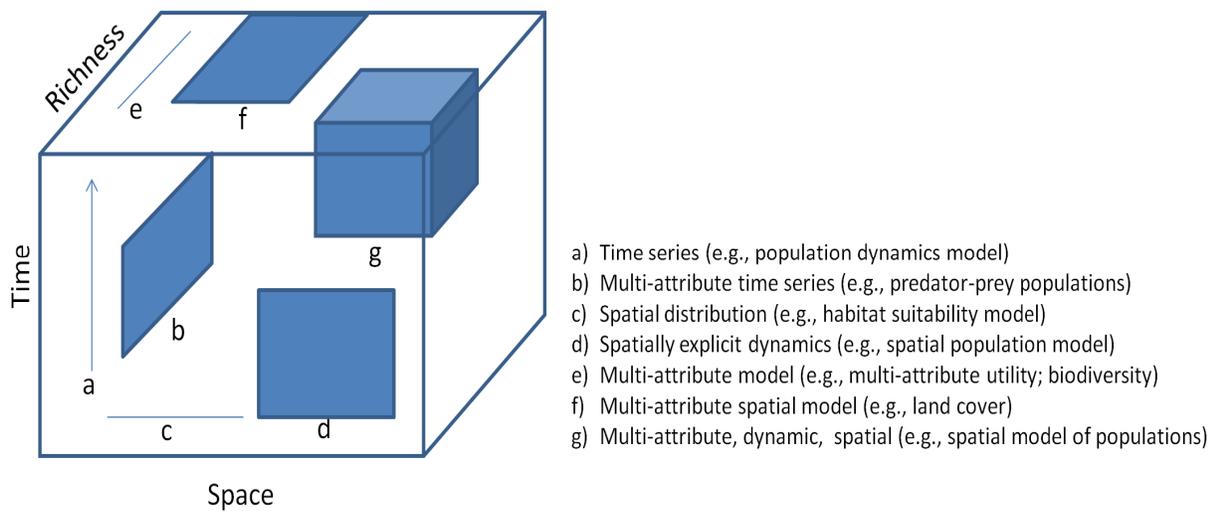


Figure 2.1: How the scoping assumptions of different types of social-ecological models partition the three-dimensional, social-ecological system under consideration.

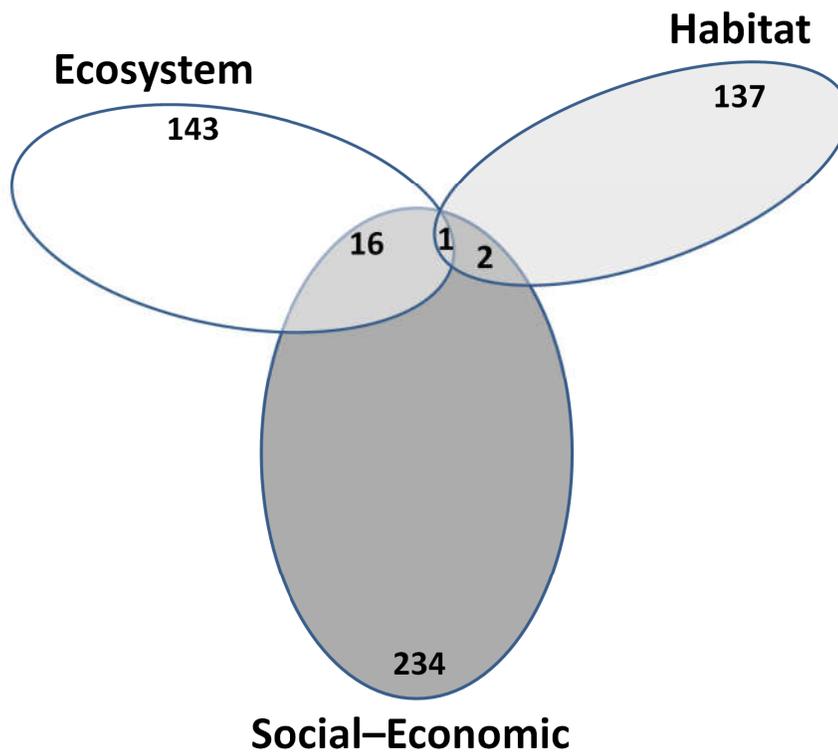


Figure 2.2: Venn diagram showing the number of articles that overlapped between the three different literature searches (areas are approximate).

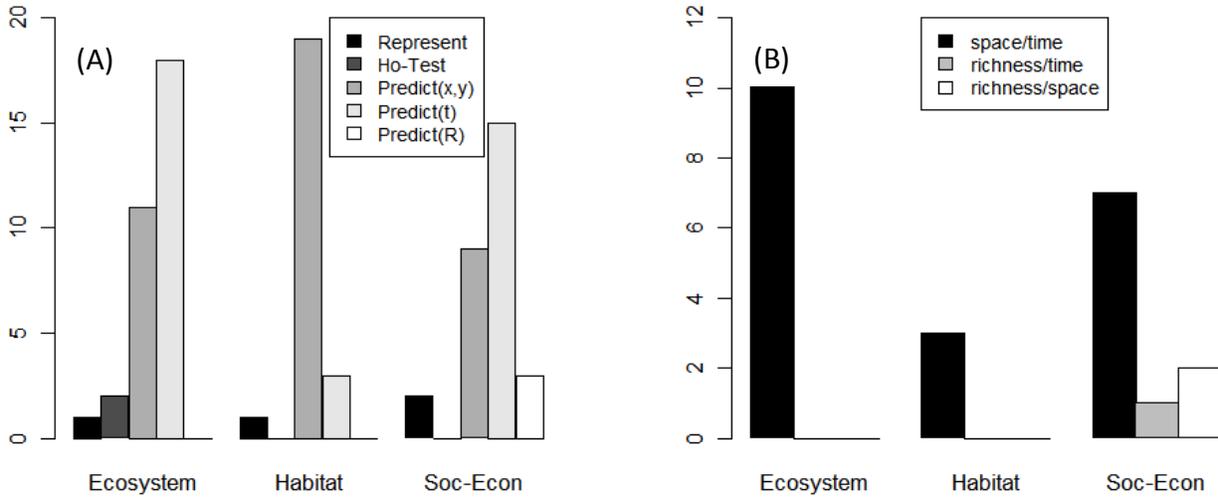


Figure 2.3: Distribution of (sometimes multiple) objectives expressed by the 60 articles evaluated showing (A) the number of objectives focused on Representation (Rep), Hypothesis testing (Hyp), and predictions across Space (x,y), Time (t), or Richness (R). For those with multiple predictive objectives, (B) shows how the three scoping axes (described in the text) were combined for each of the sectors.

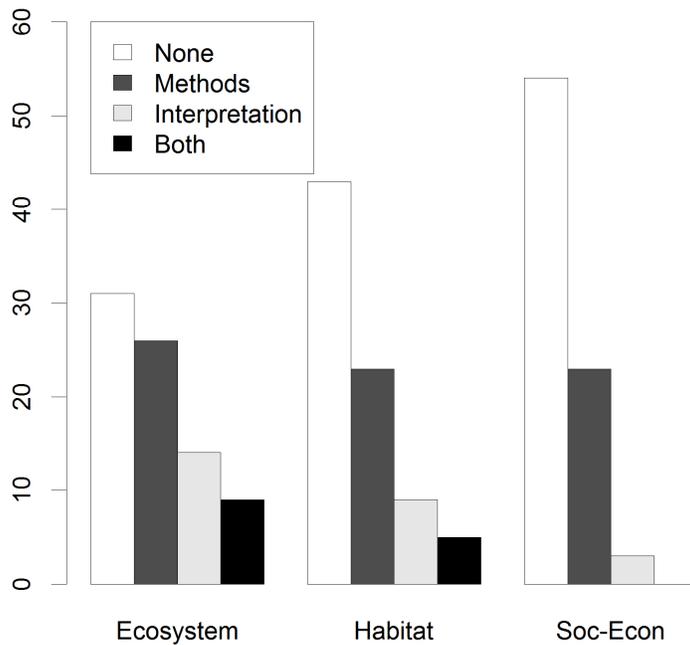


Figure 2.4: Number of papers articulating no explicit assumptions (None), at least one explicit assumption in either the Methods or Interpretation sections, or at least one explicit assumption in Both, for each of the three sector-specific searches.

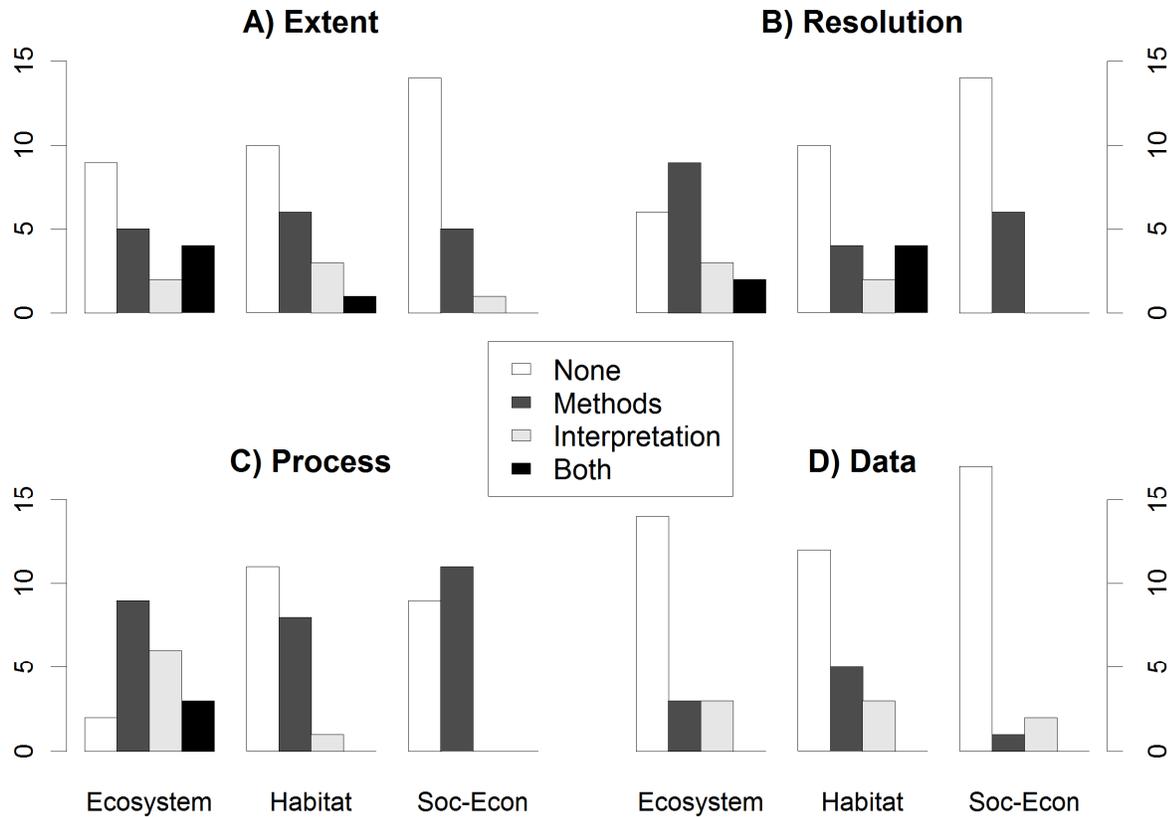


Figure 2.5: Number of papers making one or more explicit assumptions by model sector (Ecosystem, Habitat, or Social-Economic) for each of the four model design phases (Extent, Resolution, Process, and Data) described in the text.

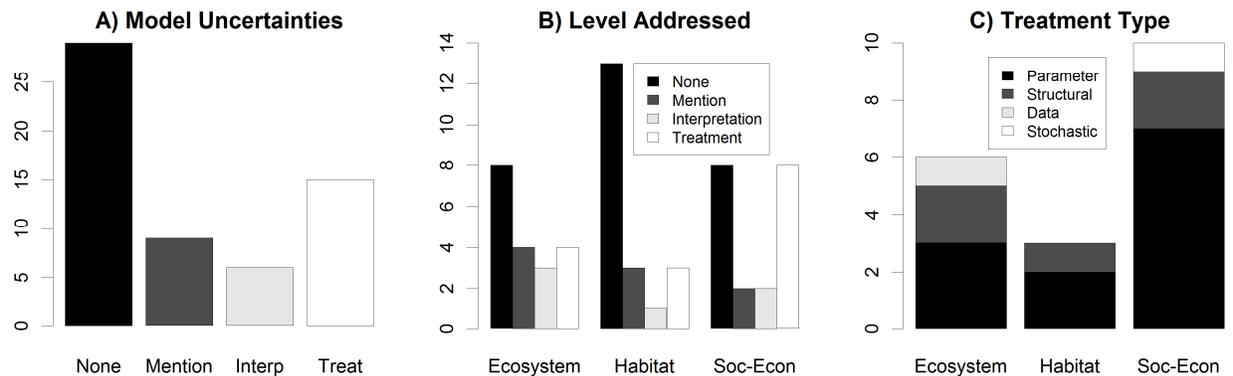


Figure 2.6: How the 60 articles considered in this review treated model uncertainty.

## **Chapter 3 - Informing kelp model complexity using independent data evaluation**

Understanding how species are distributed in the environment is increasingly important for natural resource management. Habitat models (i.e., species distribution models) are fundamental to developing this understanding, however their use in management continues to be limited. We explore several underlying challenges by contrasting the performance of a suite of kelp habitat suitability models using both common cross-validation methods and a more novel approach with independent data.

Predictions of habitat, and ultimately species distributions, are recognised as an integral component of decision support tools for ecosystem-based management, particularly marine spatial planning (e.g., Robinson et al. 2011, Schmolke et al. 2010). Understanding how species may respond to climate change is a growing part of this work (e.g., Araújo and Rahbek 2006, Sumaila et al. 2011). However, despite this clear management need, the use of habitat forecasts in management continues to be hampered by a number of significant challenges including a lack of clarity about model purpose (Araujo and Guisan 2006), inadequate evaluation methods (Vaughan and Ormerod 2005), and the continued poor treatment of uncertainty (Beale and Lennon 2012). We confront these challenges by showing how independent data can help limit model complexity and understand sampling bias, key components of model forecast uncertainty. We also discuss how these uncertainties can be more comprehensively understood with clearly articulated model objectives and assumptions.

Ecosystem models are very versatile, and can be built for description, understanding, or forecasts (Araujo and Guisan 2006). Models for description or understanding are typically built around a set of observations, with the intent of characterising the observed pattern of species distribution (Araujo and Guisan 2006). In contrast, a model for forecasting ecosystem state must consider a broader set of hypotheses about system function and, because modelling is a reductionist exercise, represent only those believed to be most important to the model objective. Unrepresented processes are assumed to be insignificant, or at least dominated by the represented ones.

Unfortunately, these design decisions, and the underlying model objectives, are rarely articulated in the modelling literature (Gegr and Chan 2014). Instead, most are left implicit, often leading to conflated objectives. For example, forecasts produced by descriptive models are regularly advanced as suitable for management despite little or no assessment of their suitability or uncertainty, presumably to valorise the model (Gegr and Chan 2014).

Whether a habitat model is predicting potential or realised habitat (Araujo and Guisan 2006) is perhaps the most challenging design decision to articulate. However, this distinction is critical for forecasts intended to support decision making because management needs can be quite distinct (Roff and Zacharias 2013) (e.g., management actions for facilitating the recovery of a species will differ from those needed to minimise impacts on existing populations).

In reality, all habitat predictions will fall on a spectrum between realised and potential, depending on the data and the ecological understanding (Jiménez-Valverde et al. 2008). It will also depend on the species, and the relative strength of its main drivers of distribution (abiotic, biotic, and movement - Soberón and Nakamura 2009). Although models of abiotic (and thus potential) habitat are by far the most abundant, progress is being made on integrating biotic and movement factors (see Normand et al. 2014 for an overview). Additionally, models intended to support very short-term management objectives (i.e., tactical models) are also achieving some success (Lewison et al. 2015), in this case by shortening the forecast horizon to weeks, thereby minimising the need for process.

The complexity of the system of interest and the myriad ways it can be represented in a model emphasises how important a clear objective is to model design, evaluation, and interpretation (Gegr and Chan 2014, Guisan and Zimmermann 2000). Evaluation methods will differ depending on whether the model is intended for understanding or prediction (Araujo and Guisan 2006).

If the model objective is understanding, cross-validation techniques are suitable for choosing the model that best fits the species distribution data (Guisan and Zimmermann 2000). Currently the most common approach to assessing habitat models, cross-validation takes a single sample of species observations and variously divides it into model training and model testing data sets.

Such analyses provide important internal verification of model performance, effectively assessing how well the model describes the sample of species observations (Araujo and Guisan 2006). While this can provide confidence in the resulting hypotheses about species-habitat relationships, this model verification tells us little about the (likely variable) quality of model predictions at other times and places (i.e., forecasts).

Forecast skill (also called transferability) essentially depends on how well a model generalises in space and time. Evaluating this is best done with independent distributional data (Guisan and Zimmermann 2000, Vaughan and Ormerod 2005). Independent data evaluation (IDE) provides a more meaningful estimate of forecast skill for two reasons. First, independent data represent an alternative ecological context in which we expect the predictive model to perform reasonably well. Perhaps more importantly, the independent data provide a more unbiased assessment because they do not share the biases of the original sample. We elaborate on this point in the discussion.

A variety of statistics can be used to compare predictions to observations (e.g., Fielding and Bell 1997), and a considerable body of literature has explored how species prevalence (the proportion of sampled sites where a species is present) can be a complicating factor (Allouche et al. 2006, Lawson et al. 2014, Mouton et al. 2010, Santika 2011) in part because of its relationship to threshold selection (Manel et al. 2001). A threshold is necessary to classify the continuous predictions typically obtained from habitat models into presences and absences so that a broader set of performance metrics derived from the resulting contingency table (also called a confusion matrix) can be calculated. Done here for the first time, I extend the study of prevalence beyond the dependent data by examining its role in independent data validation.

The above challenges all contribute to the uncertainty in model forecasts, one obvious reason why its poor treatment continues to plague ecosystem models (Link et al. 2012). Recent reviews of the habitat modelling literature (Beale and Lennon 2012, Planque et al. 2011) and ecosystem modelling generally (Gregg and Chan 2014) show a largely superficial treatment of uncertainty. In the few cases where uncertainty is examined, the focus is typically on parameterisation. Examination of uncertainties in source data, model structure, or elsewhere in

the modelling process are extremely rare (GREGG and Chan 2014, Planque et al. 2011). Without considering these broader uncertainties, estimates of model forecast skill will continue to be suspect.

We use a set of increasingly complex habitat models to illustrate how IDE can help understand structural uncertainty and sampling bias when estimating model forecasting skill. We argue that a more explicit description of model objectives and assumptions are necessary to provide a more holistic treatment of model uncertainty.

Our analysis is based on a case study of the kelp forest ecosystem in the coastal waters of the eastern North Pacific where sea otters (*Enhydra lutris*) are rapidly recovering from historic extirpation after re-introductions in the 1970s (Nichol et al. 2009). When re-occupying habitat, sea otters trigger a trophic cascade from an invertebrate-dominated to a kelp-dominated system (Estes and Palmisano 1974). This shift is viewed with mixed feelings by stakeholders because it can lead to contentious resource allocation issues (Nichol et al. 2009). Understanding how canopy kelp may be distributed after sea otter re-occupation, and the factors influencing that distribution, will be an important piece of information for management of the region's natural resources given its crucial role in coastal ecosystems (Duggins 1988).

While our study focused on habitat suitability models, the theoretical aspects associated with uncertainty apply more broadly, to any model of complex systems that seek to generate forecasts.

## **Methods**

Our study was conducted in Kyuquot Sound on the west coast of Vancouver Island, British Columbia, where sea otters have been at or close to carrying capacity for over a decade (Nichol et al. 2009). Distributional data on kelp included a survey of percent cover collected over 3 years, and 3 years of independent, presence-absence data obtained opportunistically from remote sensors. We prepared a set of abiotic predictor variables based on a review of earlier models of kelp distribution and a general understanding the factors that influence kelp distribution and abundance. We then combined the survey data with the abiotic predictors

using a series of increasingly complex habitat models for canopy kelp. We compared the resulting models using cross-validation, and evaluated their forecasting skill using an independent set of observations constructed from satellite remote sensing data. We elaborate on each of these components below.

### **Kelp observations**

We collected data on the percent cover of the two species (giant kelp - *Macrocystis pyrifera*, and bull kelp - *Nereocystis luetkeana*) that comprise the kelp canopy in the region using stratified random boat-based surveys conducted in September from 2010 to 2012. Percent cover was estimated in four quadrats within a 100-m radius of each sampling location. We also recorded the relative proportion of the two species. We sampled percent cover a total of 375 times at 173 stations over the 3 years. Resighting data (repeat visits to selected sites on later days) indicated consistent values above 5% percent cover. We therefore selected 5% as the threshold when converting to presence or absence. We simplified the survey data into a model training data set to make it comparable to the independent data used for evaluation, converting species percent cover to a simple measure of canopy kelp presence-absence.

The independent model evaluation data were derived from maps of canopy presence/absence obtained from three years (2005, 2006, and 2009) of remote sensing (RS) data. The maps were based on opportunistically collected images taken from the SPOT-5 (Satellite Pour l'Observation de la Terre) satellite-borne sensor archive. High resolution visible bands 1 through 3 were used to classify the 10 x 10 m<sup>2</sup> colour images to vegetation presence/absence using the Support Vector Machine supervised clustering algorithm (Ge et al. 2008). Six control points (areas where kelp cover was known to occur) were defined based on visual inspection and local knowledge to calibrate the classification.

### **Predictor variables**

Canopy kelp in the Pacific Northwest are understood to be influenced by bottom type, sunlight (i.e., insolation), temperature, water motion, salinity, sedimentation, and nutrient levels (Dayton 1985, Druehl 1978, 2001, Springer et al. 2007). We developed a set of predictor

variables based on this general understanding, and earlier models of kelp distribution (i.e., Bekkby et al. 2009, Gorman et al. 2013, Méléder et al. 2010).

Our study is built on a 20 x 20 m<sup>2</sup> bathymetric model of the coast. Hard substrate is critical to provide kelp a strong attachment point. However, unequivocal descriptions of bottom type, particularly near shore, are not broadly available since acoustic bottom-mapping surveys (e.g., Gorman et al. 2013) are time consuming and often spatially restricted (such surveys were unavailable in our study area). Instead, we derived rocky reefs (Reef) from the 20 x 20 m<sup>2</sup> bathymetry according to Haggarty (2015).

Insolation is important to all life history stages of kelp (Dayton 1985). Gorman et al. (2013) used mean light levels derived from satellite data, while Bekkby et al. (2009) used a proxy based on slope and aspect of the bottom. We hypothesised that in areas with high topographic relief like Pacific Canada, shading may play an important role and so constructed an insolation model using the Solar Radiation module from ArcGIS 10.2 (ESRI 2015) to estimate the potential sunlight for each 20 x 20 m<sup>2</sup> pixel in the study area. We averaged monthly insolation maps into mean summer and winter (SumSol and WinSol). We also calculated Slope and Aspect from the bathymetry to compare the proxy used by Bekkby et al. (2009) with our insolation model.

Spring growth of giant kelp has been negatively correlated with sea surface temperature (SST), assuming that SST is an inverse proxy for nutrient availability (Cavanaugh et al. 2010). However, temperature may also be physiologically limiting for canopy kelp, as Springer et al. (2007) reported an upper thermal limit for bull kelp, and Buschmann et al. (2004) reported improved early growth of giant kelp at lower temperatures. Lower SST may also be an indicator of higher O<sub>2</sub> concentrations, a potentially important factor in areas away from the higher-energy exposed coast.

Water motion, particularly through wave action, is important because of its ability to dislodge kelp from its substrate (Springer et al. 2007) and was a significant factor in all the studies on kelp distribution we reviewed (e.g., Bekkby et al. 2009, Cavanaugh et al. 2010, Gorman et al. 2013, Pedersen et al. 2012). We used fetch (Lessard et al. 2007) as an index of exposure, calculating the dominant summer (Southeast) and winter (Northwest) wind directions for

points spaced 100 m apart across our study area. We interpolated these seasonal exposure variables (FetchSE, FetchNW) to the 20 x 20 m<sup>2</sup> grid.

While excessive wave action may be responsible for dislodging plants, we hypothesised that less disruptive water movement may play a critical role in the circulation of oxygenated, nutrient-rich waters. We therefore considered the role of tidal energy using maximum bottom tidal speed (MaxTidal) obtained from Foreman et al. (2008).

Although not well studied, salinity may also affect kelp distribution, as few kelp species can tolerate low salinities (Dayton 1985). This was clearly observed during the kelp survey results, where extensive sampling closer to freshwater inputs (i.e., away from the open ocean) yielded very little kelp, although giant kelp appeared to tolerate lower salinities better than bull kelp (Gregn, personal observation). There is also evidence of a positive correlation between giant kelp spore production and salinity (Buschmann et al. 2004). In the absence of contemporaneous salinity data, we used long-term average summer bottom salinities from Foreman et al. (2008).

Finally, while sedimentation has also been identified as important for kelp habitat, we lacked suitable proxies for this factor and thus could not include it in the analysis. However, it is reasonable to assume that sedimentation is correlated with bottom type, meaning that rocky reefs by definition receive little sedimentation. We therefore assumed that sedimentation was sufficiently represented by bottom type in the models.

### **Interactions**

It is generally understood that the individual factors affecting kelp habitat do not act independently (Dayton 1985). Indeed, since ecosystems have been described as a prototypical, complex adaptive systems (Levin 1998) it would be surprising if interactions were ever truly absent from species-habitat associations. While difficult to quantify, interactions may be critical to understanding habitat suitability and the derivation of more process-based models. We tested a number of potential interactions defined using hypotheses describing how different abiotic variables could potentially combine to improve kelp habitat quality.

1) Slope and Aspect. We elaborated on Bekkby et al.'s (2009) use of these two variables as a proxy for sunlight by testing if interaction terms were more effective predictors of kelp.

2) Exposure and SST. These variables are inversely correlated with distance from shore and also appear to have opposite effects on kelp habitat suitability. Cavanaugh et al. (2010) found the response of giant kelp biomass dominated by wave disturbance in exposed regions, while SST was more dominant in sheltered regions. Such regional heterogeneity strongly suggests an interaction between SST and exposure.

3) Exposure and Salinity. In contrast to SST, salinity is positively correlated with distance from shore and exposure. However, we hypothesised that the importance of elevated salinity would vary with exposure, perhaps playing a more significant role in low exposure areas.

4) Slope and MaxTidal. Tidal energy circulates and mixes water quality characteristics; slope can serve as both a proxy for bottom type and a component of insolation. We hypothesised that the role of tidal energy differed in regions with low and high slope.

### **Model development**

Habitat models range in complexity from the straightforward habitat suitability index (HSI) approach pioneered in the 1980s by the US Fish and Wildlife Service (Van Horne and Wiens 1991) to sophisticated regression and machine learning methods that are very adept at creating complex relationships to capture nuanced patterns in the data (reviewed by Merow et al. 2013). Studies comparing the relative performance of the various methods appear regularly (e.g., Elith et al. 2006, Guisan and Zimmermann 2000, Pearson et al. 2006, Segurado and Araújo 2004). Generalised linear models (GLMs) and generalised additive models (GAMs) are the two most common regression methods used today, and they consistently rank among the best for correlating abiotic predictor data with species observations. While machine learning methods are increasingly popular (Merow et al. 2013), their potentially high complexity can lead to ecologically meaningless relationships (Gregg 2011, Merow et al. 2013), unsuitable for forecasting.

The "best" method to apply likely depends on the model context and intent (Segurado and Araújo 2004). Our intent here was to evaluate forecasts from a set of models with increasing complexity, with the complexity explicitly tied to ecological process. We therefore began by reviewing both the ecological understanding of kelp distributions and the available abiotic data (i.e., predictors), making explicit hypotheses about how the predictors may influence kelp distributions. We used these hypotheses to define our simplest model using the HSI approach. We then examined the strength of association between each potential predictor variable and our survey data using univariate GLMs. We considered linear, quadratic, and cubic forms, and applied this analysis to the presence-absence of each component species (i.e., giant and bull kelp) as well as to the combined canopy.

Using the predictors identified as significant based on the univariate GLMs, we applied a structured variable selection approach to create 5 additional statistical models with increasing complexity. We first defined a GLM model using only the linear terms for the significant variables. We then used Akaike's Information Criterion (AIC) to test whether increased model complexity was warranted, considering first higher order polynomials for those variables where significance was implied by the univariate analysis; second, any predictors identified as significant for the individual species; and third, a final set of more complex models containing potential interactions terms. At each step, the best model was selected using AIC after considering both single term addition, and single term removal. A final inspection ensured all terms in the GLM model were significant at the 0.05 level or better. This structured approach ensured the predictors with the highest explanatory power entered the models first, and that all included predictors contributed significantly to model performance. This structured use is fundamentally different from the automated model-building approach understood to have a range of methodological problems (Whittingham et al. 2006). We then created two GAMs, the first with a complexity equivalent to the most complex GLM, and the second with a maximum complexity. This allowed us to compare and contrast how model structure related to performance (i.e., whether the GAM could explain more variance than the GLMs). All models were constructed using a binomial link function.

We represented all data in an equidistant projection (BC Albers Conic), and mapped all predictor variables to the 20 x 20 m<sup>2</sup> bathymetric grid. Lower resolution variables (SST, Salinity, MaxTidal) were re-sampled to this working resolution. All data analyses and visualisations were performed in the R language for statistical analysis (R Core Team 2015) using the add-on packages mgcv (Wood 2004) and AUC (Ballings and Van den Poel 2013) for analysis, and dplyr (Wickham and Francois 2015), and ggplot2 (Wickham 2009) for presentation of results.

### **Evaluating the models**

In the development of the statistical models, we compared their relative performance using deviance explained ( $\Delta D$ ). This statistic is typically used for GLM and GAM models and is analogous to variance explained (i.e.,  $R^2$ ) in linear models (Guisan and Zimmermann 2000).

We verified each model structure using a randomised cross-validation test (Fielding and Bell 1997). We bootstrapped 1000 samples of randomly selected training (2/3) and testing (1/3) partitions (carefully preserving the prevalence of the original survey data) and calculated the distribution of Area Under the Curve (AUC) scores. AUC is a widely used, threshold-independent measure of model performance (Fielding and Bell 1997), where a score of 1.0 implies perfect prediction, while 0.5 implies predictive power no better than random.

To evaluate the forecast skill of the 6 increasingly complex models built using the kelp survey data, we compared their predictions to the 3 years of independent RS data. We compared the model forecasts to the individual years and to the cumulative presence over all years. Because the RS data were spatially comprehensive, we were able to simulate the field collection at different prevalence levels by drawing 100 samples of 500 observations from each year of RS data, repeated for 5 different prevalence levels ranging from a low of 0.03 (observed in the sparsest year of RS data) to 0.50, the average prevalence observed across the 3 years of survey data. Finally, we examined how the sensitivity (true positive rate) and specificity (true negative rate) components of the AUC responded to prevalence, since examining the components of AUC may help understand model performance (Lobo et al. 2010). To avoid complicating our analysis with the question of threshold selection, we used AUC and bi-serial correlation (COR), also a threshold-independent metric, which describes the correlation between model

predictions and observed presence/absence, and is seen as complimentary to the AUC (Elith and Graham 2009).

## **Results**

### **Model structure**

We defined our HSI model according to Depth, Reef, SST, MaxTidal, FetchSE, and Salinity. We hypothesised canopy kelp habitat suitability increased with the probability of rocky reefs, salinity and tidal energy, and inversely with temperature and FetchSE (exposure) (Fig. 3.1). We distinguished between essential factors (those that were necessary for habitat) and quality factors (those hypothesised to improve habitat quality) and represented them using multiplication and addition respectively.

Our univariate GLM analysis of all individual predictors formed the basis of our statistical analysis. These initial estimates of predictor importance largely mirror earlier findings from the literature, with Depth, Slope, Reef, SST and exposure (both FetchSE and FetchNW) all identified as significant (Table 3.1). We also found Salinity to be highly significant to the canopy in general, and to giant kelp in particular, a factor not considered in the earlier studies but presumably relevant in regions such as the Pacific Northwest with an abundance of freshwater input, embayments, and fjords.

Using this information, we created progressively more complex GLMs until no further reduction in AIC could be achieved. The deviance explained ( $\Delta D$ ) increased from 0.39 in the simplest GLM (GLM0), to 0.56 in the most complex (GLM3c; Table 3.2). The biggest decreases in AIC resulted from the addition of higher-order (quadratic and cubic) terms (GLM1 and GLM2), followed by the inclusion of interaction terms (Table 3.2). However, AIC became somewhat equivocal once we began to include multiple interactions. Thus, when moving from GLM2 (the best model with higher-order terms but no interactions) to GLM4 (the best overall model), we also considered the significance of the variables included in the model. This allowed us to choose between interactions with similar effects on the AIC (i.e., GLM3c vs. GLM3b).

Specifically, the interactions Exposure:SST and Exposure:Salinity yielded almost identical changes in AIC and  $\Delta D$ . A high negative correlation (-0.50) between SST and Salinity warranted dropping one of the terms. We found that simplifying the SST term (from quadratic to linear) resulted in a higher number of significant variables in the model containing the Exposure:SST interaction, giving us our final model (GLM4) which had slightly higher AIC, but contained only significant ( $p < 0.05$ ) terms.

We tested the explanatory power of both insolation models before and after adding the other interactions. In no case did an explicit insolation model generate more than marginal reduction in AIC. Lastly, we tested the Slope:MaxTidal interaction and found it provided marginal model improvement. Since all variables remained significant, we retained this interaction.

We then constructed the two GAM models by specifying their complexity using the  $k$  parameter (see Table 3.2). The first (GAM1) contained the same terms, interactions, and degrees of freedom as GLM4, thus representing the non-parametric (i.e., smoothed) equivalent of the best GLM model. The second GAM (GAM2) represented the most complex model in our analysis, and was created by extending GAM1 with as many degrees of freedom as the AIC criterion would admit.

### **Model performance**

We compare and contrast the explanatory power of three GLM models (GLM0, GLM2, and GLM4) with the two GAM models. The model performance statistics (AIC and  $\Delta D$ ) changed predictably as complexity was added to the GLM models (Table 3.2). However GAM1, while an analog of GLM4, had AIC and  $\Delta D$  scores more comparable to the less complex GLM2 model. For GAM2, the  $\Delta D$  was equivalent to GAM4, but the AIC of was lower because of the higher number of parameters.

The cross-validation of the five statistical models showed high and similar AUC scores (0.86–0.91) (Table 3.3). The AUC of the HSI model (0.54) suggested performance no better than random. In contrast to this internal verification, the AUC scores of the model forecasts evaluated using the independent test data were notably different.

Mean forecast skill averaged over 3 years of RS data and 5 prevalence levels (Fig. 3.2) indicated that the HSI and GLM0 models has similar but poor skill. The highest skill was achieved by GLM2 (higher order terms but no interactions), followed by GAM2 and GLM4. Results for AUC and COR were highly correlated; we therefore report results for AUC only.

The individual effects of prevalence and year on the performance metrics showed significant differences (Fig. 3.3). Forecast skill peaked at intermediate prevalence values for all models, with the highest prevalence (0.5) showing the greatest variability across years (Fig. 3.3a).

Variability in prevalence within years (Figs. 3.3b) showed a somewhat more consistent pattern with forecast skill increasing from 2005 to 2009 across all models (with the exception of GLM0). In addition to producing the lowest skill, 2005 also showed the highest variability across prevalence values. Model skill was generally higher when the years were aggregated.

The relative forecast skill of the different models observed for the average across years and prevalence values (Fig. 3.2) persisted when examined in more detail. Forecasts from the GLM2 model was as good as or better than all other models, in all comparisons, although the difference between GLM2, GLM4, and GAM2 were negligible in most cases. Importantly, the forecast skill of the simplest model (HSI) was as good or better than both GLM0 and GAM1 (Fig. 3.3).

Decomposing the AUC score into its component parts (Fig. 3.4) illustrates how prevalence influences specificity and sensitivity directly. Specificity was generally low, but peaked at a prevalence of 0.2. Sensitivity was the main driver of the AUC score, peaking at a prevalence of 0.09 before dropping off. The prevalence of the stratified survey data used to build the models ranged from 0.40 to 0.55 across the 3 years, while in the classified remote sensing images prevalence ranged from 0.03 to 0.06.

## ***Discussion***

The primary objective of this study was to develop a reasonable habitat model of canopy kelp habitat in Pacific Canada. We also contrast model validation, achieved by re-sampling a single data set, with model evaluation (of forecast skill) using external, independent data. We show

how model evaluation can identify the practical limits of model complexity, and how assessing the results in the context of explicitly stated model objectives and assumptions can provide a more complete picture of the uncertainty in model forecasts.

Our models of canopy kelp distribution confirmed that the abiotic predictors identified by studies of other kelp species, in other regions, are also important in the Canadian Pacific. These include depth, bottom type, bottom slope, exposure, tidal flow, and insolation. We also identified salinity as a potentially important predictor, particularly for giant kelp, an effect that may be prevalent in areas with a complex coastline and significant fresh water input.

While the process underlying some of these predictors is clear (e.g., bottom type, exposure), the role of others (e.g., depth) is more equivocal, in that they may serve as proxies for other, more proximate variables. How well the ecological function of predictor variables can be characterised is essential to a model's forecasting skill (Austin 2002). The quest to identify more proximate ecological predictors was the motivation behind our exploration of variable interactions.

Despite the obvious importance of insolation and the likely role of depth as a proxy, our model of insolation did not explain sufficient variability to displace depth in the models. However, our approach led to the inclusion of slope and aspect independently prior to our evaluation of interactions. Given their potential for capturing insolation (Bekkby et al. 2009), their presence in the models likely precluded the entry of our insolation model.

Nevertheless, the importance of considering interactions is illustrated by our exploration of the role of exposure with water-column properties (i.e., temperature and salinity). Both this interaction, and that between topography and water movement (i.e., slope and tidal flow), provide potentially important refinements to descriptions of kelp habitats in nearshore ecosystems. Further exploration of these interactions would likely clarify the role of these variables, leading to the identification of more proximate predictors, and improved model forecast skill.

## **Model structure and performance**

Our structured approach to model development including using standard criteria (i.e., AIC) as a stopping condition for model complexity resulted in a model (GLM4) with interactions and higher order terms. The GAM1 model (the smoothed representation of GLM4) was unable to explain as much of the deviance ( $\Delta D$ ) in the survey data despite its higher complexity (based on degrees of freedom used). The model ranking based on  $\Delta D$  was mirrored by the AUC scores from cross-validation.

Under IDE, mean AUC scores were considerably lower for all the statistical models. Vaughan and Ormerod (2005) suggest such a drop in AUC from training to testing data is likely attributable to what they term transportability. This is effectively the assumption that the processes captured by the model are stationary (i.e., invariant) across time and space. This assumption is problematic in heterogenous habitats (Wagner and Fortin 2005), as discussed below.

IDE also produced a different rank order than cross validation, with the moderately complex GLM2 showing the best mean performance and significantly outperforming its comparable GAM1 model. Comparable forecasting performance by the GAMs was obtained only by dramatically increasing the number parameters (i.e., GAM2).

A closer look at the models suggests that one reason GAM2 performed as well as it did was because it fit a subset of dominant drivers (e.g., Depth, Reef) extremely well, while the GLMs relied on less precise fits across a larger number of predictors, yielding a poorer fit to training data but better forecasts. The same reasoning explains why the GAM1 model did not perform as well as its GLM equivalent. This strongly suggests that fitting to data with an equivalent number of degrees of freedom results in less generalisable relationships. This applies equally to GAMs and other pattern-matching approaches (e.g., machine learning), and also explains why these methods have a tendency to over-fit the data, creating ecologically implausible relationships (Gregr 2011, Merow et al. 2013, Warren and Seifert 2011). Thus, in addition to generalising better than GAMs (Randin et al. 2006), and thus having higher forecasting skill,

rationally constructed parametric GLMs models are easier to explain (Wintle et al. 2005), making them more ecologically defensible.

We argue that an emphasis on cross-validation is the primary cause of model over-fitting, as models strive to maximise their description of the data on which they are based. Focusing on maximising internal validation metrics instead of realistic representation of process can result in significant, and often unnecessary model complexity, particularly for non-parametric methods (Merow et al. 2013). This is somewhat troubling given what should be a general understanding that high complexity is no guarantee of high forecast skill, and may even reduce it (Costanza and Sklar 1985, Fulton et al. 2003). A reliance on cross-validation undermines the essential need to balance complexity and generality. We therefore urge modellers to instead focus on IDE approaches where possible, and when independent data are not available, avoid confusing model validation with evaluation (forecasting skill).

This re-enforces how important understanding process is to models intended for forecasts. If models are fit to data without ecological consideration, relevant biotic or anthropogenic interactions will almost inevitably be overlooked (Palacios et al. 2013, Soberón and Nakamura 2009). GLMs provide an explicit means of focusing on known proximate variables, and provide a coherent way to include higher-order terms and interactions.

Further evidence that simpler models can lead to better forecasts is our finding that the hypothesis-based HSI (which was not fit to data) in some circumstances scored as well or better against the independent data than both GLM0 and the much more complex GAM1 model. This illustrates what can be accomplished with a simple process-based model if the system is reasonably well understood. While poor at predicting the survey data, it proved generalisable enough to track and sometimes outscore the statistical models across the different evaluation data sets. While no substitute for an analysis that is both ecologically based and empirical, such process-based models can provide a reasonable starting point for estimating species' habitats, particularly in data-poor contexts. Equally important is that they may well outperform empirical models when the training data are excessively biased (see below).

## **Representativity**

The question of representativity (i.e., bias) applies to both the observations of species distributions and the predictor data. Habitat suitability models largely continue to use opportunistically collected observations of species distributions, and these data are understood to often contain spatial sampling bias (Phillips et al. 2009). However, the inter-annual variability observed in our measures of model forecast skill (Fig. 3.3b) led us to consider the role of temporal sampling bias, something not widely considered in habitat suitability modelling.

Canopy kelp distribution changes both seasonally and annually. We focus here on the peak distribution at the end of the summer growing season, and how this may change from year to year. Edwards and Estes (2006) linked inter-annual variability in giant kelp abundance to El Niño events. In Pacific Canada, cooler (La Niña) years generally lead to higher winter storm frequency on the coast (NOAA 2015b), suggesting a higher potential for kelp forest destruction during La Niña years. Using the ONI (Oceanic Niño Index - NOAA 2015a), we found our survey data (2010 to 2012) corresponded to a cool phase of the ONI, and 2 years of the RS data (2005, 2006) corresponded to a warm phase, while 2009 was part of a cooler phase. The higher observed prevalence in the 2009 RS data (3 and 1.5 times higher than 2005 and 2006 respectively) supports the hypothesis that there is less canopy kelp following a La Niña winter.

Our models (built using data from a cool phase) evaluated well against the aggregated kelp presence (i.e., 'all' in Fig. 3.3b) and also against the 2009 sample, but performed notably less well against the years from the warm ocean climate regime (2005/06).

Such variability is obscured when species distribution data are aggregated over time, because aggregation removes inter-annual variability, biasing estimates of forecast skill by assuming that the ecological context of the training data is representative of the long-term average. The difference between the actual training sample context and the long-term average can be termed the temporal sampling bias, and its magnitude can be inferred from how well the model forecasts evaluate against the different years of testing observations. This shows that temporal bias can be an important component of the forecast uncertainty, analogous to the role played by initial conditions in simulation models (Fulton et al. 2003, Gibson and Spitz 2011).

Gregr (2011) noted that combining multiple years of observations with long-term climate averages removes inter-annual variability, retaining only the more persistent, long term signals in the data that are indicative of a species' potential habitat. Our results corroborate this assertion, and suggest that longitudinal data representative of the range of ocean climate are necessary to build an accurate model of potential habitat. This aligns with the preferred way of measuring a model's generalisability, which is to collect evaluation data from the range of proposed applications (i.e., different times and places), thereby simulating its use (Vaughan and Ormerod 2005).

A desire to forecast annual distributions indicates a shift in model objectives towards predicting realised habitat. In our case, this implies the need for an index of annual storm intensity or frequency to capture the hypothesised dynamics. Adding such data would remove the assumption of representativity and the associated temporal sampling bias. We note, however, that the increased model complexity could add to both parametric and structural uncertainties, emphasising the trade-off between complexity and generality.

The risk of extrapolation across space or in time is very real for forecasts of realised habitat. This emphasises the need for forecast horizons (Petchey et al. 2015) to help determine the distance (either spatial or temporal) to which a forecast can be expected to be reliable. Dorman et al. (2008) found that model type and data quality had the greatest influence on temporal forecasts of species distributions. Thus, understanding temporal sampling bias in habitat model forecasts is likely to help identify such horizons.

The role of representativity in the predictor variables is also under-represented in discussions of habitat suitability models. This is a question of how to scale (i.e., average) dynamic variables. Models are often built with climatologies or by associating species observations with temporally concurrent data. In the context of understanding, using contemporaneous physical data is reasonable and can often lead to high correlations. However translating such relationships into forecasts of realised distributions begs the question of how to scale the predictor to create the forecast. Predictors are often re-scaled to an annual (for example) resolution, but this tends to diminish the strength of the relationship. A better approach might

be to create a series of models at a reasonable time step (i.e., monthly) and use model averaging to estimate the realised distribution. While likely preferred over the re-scaling of predictors, this would require a time-series of observations.

This is fundamentally a question of representing the presumed ecological process appropriately, and is essentially a re-phrasing of the scaling challenge articulated by Weins (1989). Observations must be representative of the model objective, and predictors must properly represent the ecological context of the observations (GREGG 2011, Montalto et al. 2014).

The question of representativity also applies to the myriad relationships represented in the model structure and parameterisation. This idea of stationary processes is perhaps the biggest challenge facing ecological forecasting tools, particularly when models are developed less on understanding and more on correlation (Palacios et al. 2013). While methods for treating non-stationarity in correlative models are emerging (e.g., Austin 2007, Beale et al. 2014, Wagner and Fortin 2005), they are yet to be widely applied.

### **Prevalence, sensitivity, and specificity**

We varied the prevalence of the evaluation data in our analysis because of published concerns about its effects on model performance. By simulating presence/absence sampling from the RS data at various prevalence levels we were able to show how model forecast skill varies with the prevalence of the evaluation data (Fig. 3.3a). The prevalence resulting in the best forecast skill (0.09) was marginally higher than the observed prevalence in the RS testing data, but much lower than the 0.4-0.55 observed in our stratified sample of training data.

Since we did not control for representativity (an even distribution of the data across environmental and geographic gradients) of the RS testing sample, some of the observed variability can likely be attributed to this random selection. However, while Jiménez-Valverde (2006) found the effect of prevalence to be negligible in model training data, our results imply an optimum prevalence in the evaluation data that result in the highest AUC and COR scores.

Our examination of how specificity and sensitivity responded to prevalence shows that sensitivity - the model's ability to forecast absence - was the main driver of the AUC score. The GLM2 predicted presence best at intermediate prevalence values, while absences were most accurately predicted at lower prevalences. This result supports other calls for a wider range of disaggregated performance statistics focused on specificity and sensitivity rather than integrated measures such as AUC (Lobo et al. 2010).

### **Assumptions and uncertainties**

To be meaningfully assessed, model forecast skill must be considered in the context of model objectives (Araujo and Guisan 2006, Guisan and Zimmermann 2000). The desire for models to meet multiple objectives confounds their assessment, damaging the credibility of habitat modelling in particular and ecosystem modelling more broadly. Perhaps the most egregious misrepresentation of objectives has been the recent trends in re-framing habitat suitability models as species distribution models. While it may seem trivial to quibble about semantics, precision of language is important since some audiences will interpret language literally. This trend not only misrepresents the work done, but downplays both the challenges faced by the modelling community and the importance of habitat itself, and gives the impression that our forecasts are better than they are.

Given that the interpretation of quantitative performance measures as good or bad depend on context (Jiménez-Valverde et al. 2008), articulating this context is the first step in communicating the confidence warranted in the model. This context includes both the ecological realism of the predictors, and the rationale for the underlying model design decisions.

Explicit statements of the hypotheses represented in models for forecasting are also essential to engender confidence in the model predictions. Our investigation of the role of sunlight, for example, emphasises the ways it is and can be represented in models, contributing to our understanding of both the process, and its representation. This question of what to include and how to include it is a critical aspect of model design, and relates directly to structural

uncertainty (GREGG and Chan 2014). Models also include assumptions about the quality of the data used to build the model (related to prevalence and representativity).

Such assumptions and the confidence we should have in them appear to be rarely re-visited after the initial model design, yet assumptions will comprise a significant portion of the uncertainty in any model forecast. Articulating our objectives, the ecological context where we expect our forecasts to be relevant, the ecological processes that are (and are not) represented, and the biases in our data can provide a more holistic sense of the overall model uncertainty. This is essential for conveying the overall confidence that can be placed in model forecasts, something that is currently beyond the reach of quantitative uncertainty assessments.

### ***Conclusions***

To be useful for decision making, model forecasts must be clear on what they are predicting, and articulate both the ecological context to which they apply, and the confidence that can be placed in them. Quantitative assessments of uncertainty in model structure and parameterisation advance understanding by providing insight into model validity. However, confidence in model forecasts depends more on the holistic consideration of assumptions and uncertainty relating to the many aspects of model design. This includes the representativity of both the training and testing data, the suitability of the predictor variables, and the assumptions of process that relate the data to the model context.

We echo calls for models of intermediate complexity because their generality makes them more appropriate for forecasting, and because they are easier to interpret and assess. We argue that parametric models (e.g., GLMs) are more interpretable than those derived through machine learning, partially due to their parametric description, but also because they require the analyst to consider ecological processes a priori. We have also shown that GLMs can represent the full range of ecologically reasonable functional forms, and allow more straightforward inclusion of interactions among processes. While not generally considered or applied in practice, interactions are a potentially important, under-studied aspect of habitat.

Cross-validation methods are useful for understanding how well we match observations, but less so for understanding the quality of our predictions. By subsampling data from a single sampling context, using a single model structure, cross-validation essentially provides a description of parametric uncertainty within a single ecological context. This is appropriate when developing a descriptive model or evaluating process hypotheses, but is clearly inadequate for evaluating model forecasts which by definition must be measured by how well they perform in different ecological contexts.

Model forecast skill is best evaluated using independent data, within a well-articulated description of the ecological, model, and data sampling contexts. Evaluation with independent data provides a quantitative way of balancing model complexity and generality, identifying the model forecasts that best correspond to the independent data, and thus identifying the most appropriate model complexity for the context at hand.

We have used the above approach to show that temporal sampling bias (e.g., sampling only in an El Niño year) has as much potential to influence model forecasts as its more commonly considered sibling, spatial bias. This is true even for models with no temporal resolution, since sampling bias - whether spatial or temporal - can exert an initial conditions effect on forecasts of habitat suitability.

In cases where the training data are strongly biased either spatially or temporally, the forecast skill of simpler, process-based models (e.g., HSI) may exceed that of more complex models. Process-based models will also provide considerable utility in the absence of species observations. Evaluations with independent data, not internal verification, are the most appropriate way to assess forecasts from such models.

Evaluating forecasts from multiple model structures using independent data, and the development of more holistic approaches to articulating model uncertainty, will increase the utility of model forecasts for decision-making. While still not a comprehensive treatment of uncertainty, without some progress on this front our models will (and should) remain largely outside the policy and decision-making sphere.

Table 3.1: Significance levels( $p$  values: "\*\*\*\*" < 0.001; "\*\*\*" < 0.01; "\*\*" < 0.05; "." < 0.1) for the univariate relationships between linear, quadratic, and cubic polynomial forms of the proposed predictor variables and the presence/absence of Kelp Canopy and its two component species Giant and Bull kelp. See text for variable descriptions.

Model	Variable	Linear	2nd order	3rd order
Canopy	Depth	***	--	--
	Slope	***	**	**
	Aspect	--	--	--
	Reef	***	--	.
	SST	***	***	--
	sstQ2	--	--	--
	sstQ3	--	**	--
	Salinity	***	--	*
	SumSol	--	--	--
	FetchSE	*	.	*
	FetchNW	***	***	***
	MaxTidal	--	--	--
	Giant kelp	Depth	***	--
Slope		***	.	**
Aspect		**	--	--
Reef		*	--	--
SST		***	--	--
sstQ2		--	***	--
sstQ3		--	***	--
Salinity		.	**	***
SumSol		*	--	--
FetchSE		--	--	--
FetchNW		.	--	.
MaxTidal		--	--	***
Bull kelp		Depth	**	--
	Slope	**	***	**
	Aspect	*	--	--
	Reef	***	--	--
	SST	***	***	--
	sstQ2	--	--	--
	sstQ3	--	--	--
	Salinity	--	--	--
	SumSol	--	--	--
	FetchSE	.	.	--
	FetchNW	*	*	*
	MaxTidal	--	--	--

Table 3.2: Results of model development showing model terms, AIC scores, and deviance explained ( $\Delta D$ ) with increasing model complexity. First column shows the model names used in the comparative analysis. See text for description of variables and methods.

	Model Scope	AIC	$\Delta D$
<i>GLMs</i>			
<b>GLM0</b>	Depth + Reef + Salt + Slope + SST	326.7	<b>0.39</b>
GLM1	Depth + Reef + Slope <sup>3</sup> + SST <sup>2</sup> + Salt <sup>3</sup>	306.8	0.45
<b>GLM2</b>	Depth + Reef + SST <sup>2</sup> + Slope <sup>3</sup> + Salt <sup>3</sup> + Aspect + maxTidal <sup>2</sup> + FSElog <sup>2</sup>	302.2	<b>0.48</b>
GLM3a	Depth + Reef + (SST <sup>2</sup> * FSElog <sup>2</sup> ) + Slope <sup>3</sup> + Salt <sup>3</sup> + Aspect + maxTidal <sup>2</sup>	281.0	0.53
GLM3b	Depth + Reef + (SST <sup>2</sup> * FSElog <sup>2</sup> ) + Slope <sup>3</sup> + (Salt <sup>3</sup> * FSElog <sup>2</sup> ) + Aspect + maxTidal <sup>2</sup>	276.6	0.56
GLM3c	Depth + Reef + (SST <sup>2</sup> * FSElog <sup>2</sup> ) + (Slope <sup>3</sup> * maxTidal <sup>2</sup> ) + Salt <sup>3</sup> + Aspect	276.1	0.56
<b>GLM4</b>	Depth + Reef + (SST * FSElog <sup>2</sup> ) + (Slope <sup>3</sup> * maxTidal <sup>2</sup> ) + Salt <sup>3</sup> + Aspect	277.0	<b>0.55</b>
<i>GAMs</i>			
<b>GAM1</b>	Depth + Reef + s(SST*FSElog, k=5) + s(Slope*maxTidal, k=6) + s(Salt, k=3) + Aspect	298.4	<b>0.48</b>
<b>GAM2</b>	Depth + Reef + s(SST*FSElog, k=10) + s(Slope*maxTidal, k=10) + s(Salt, k=9) + Aspect	282.6	<b>0.54</b>

Table 3.3: Cross-validation of kelp models showing AUC and standard error (SE) for the six increasingly complex habitat models described in the text and in Table 3.2.

Model	AUC	SE
HSI	0.54	1.33E-03
GLM0	0.86	8.55E-04
GLM2	0.89	7.77E-04
GLM4	0.91	7.20E-04
GAM1	0.88	7.96E-04
GAM2	0.89	8.29E-04

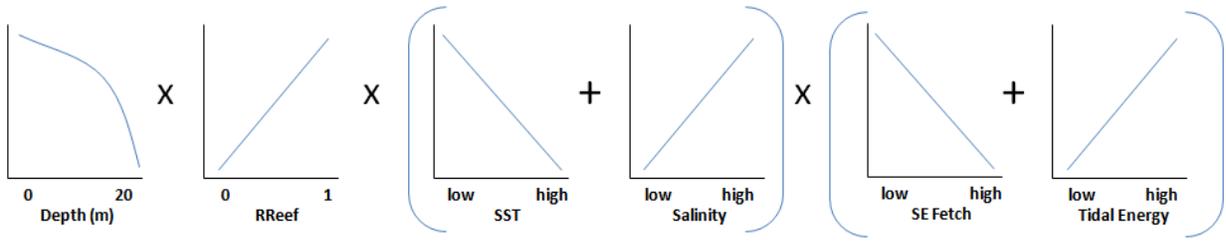


Figure 3.1: The structure of the HSI model for canopy kelp showing how the relationships between individual predictors and habitat suitability were combined.

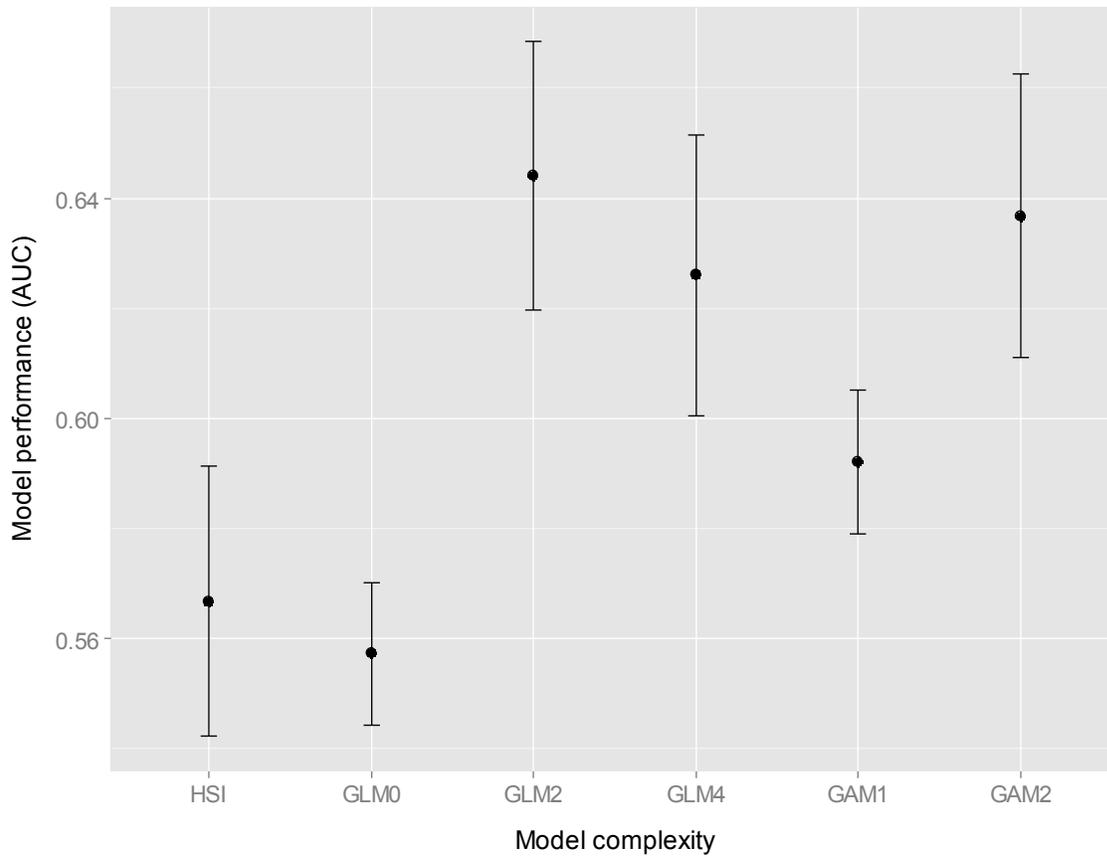


Figure 3.2: Model performance (AUC) for the 5 increasingly complex models based on 3 years of independent data. Confidence intervals are based on evaluation with 5 prevalence levels.

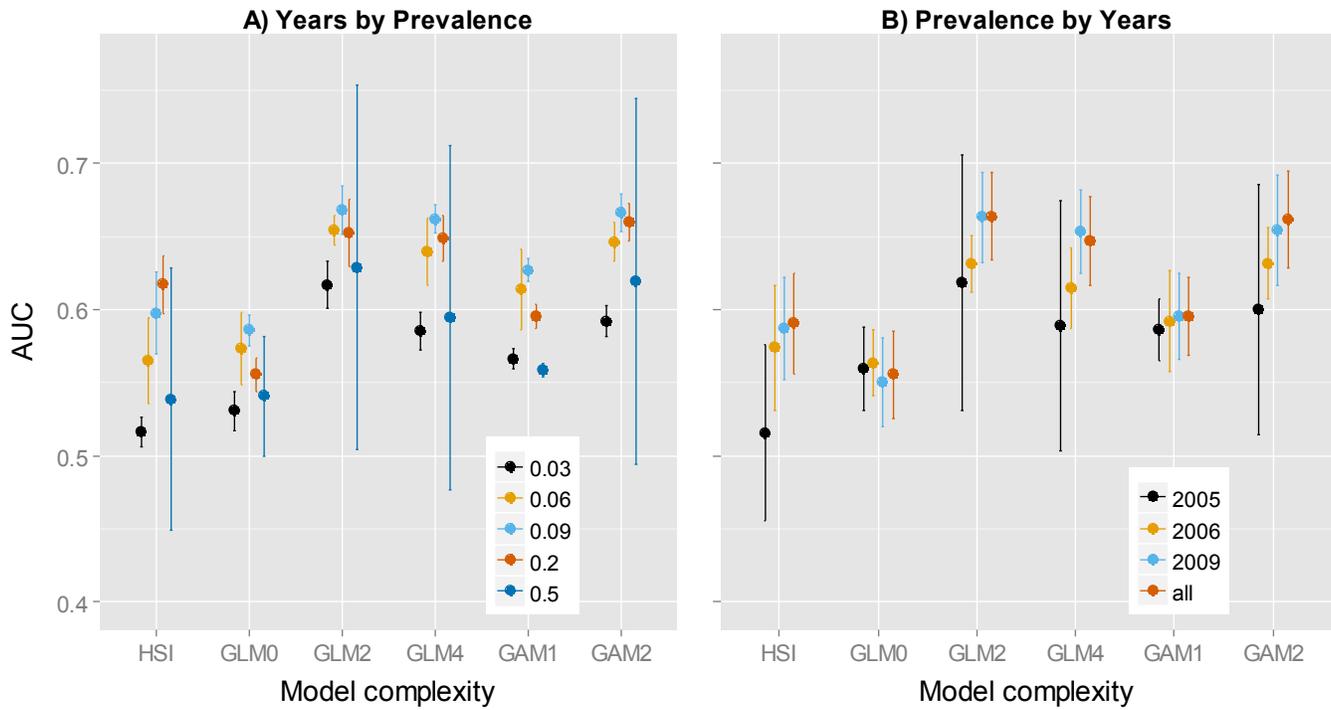
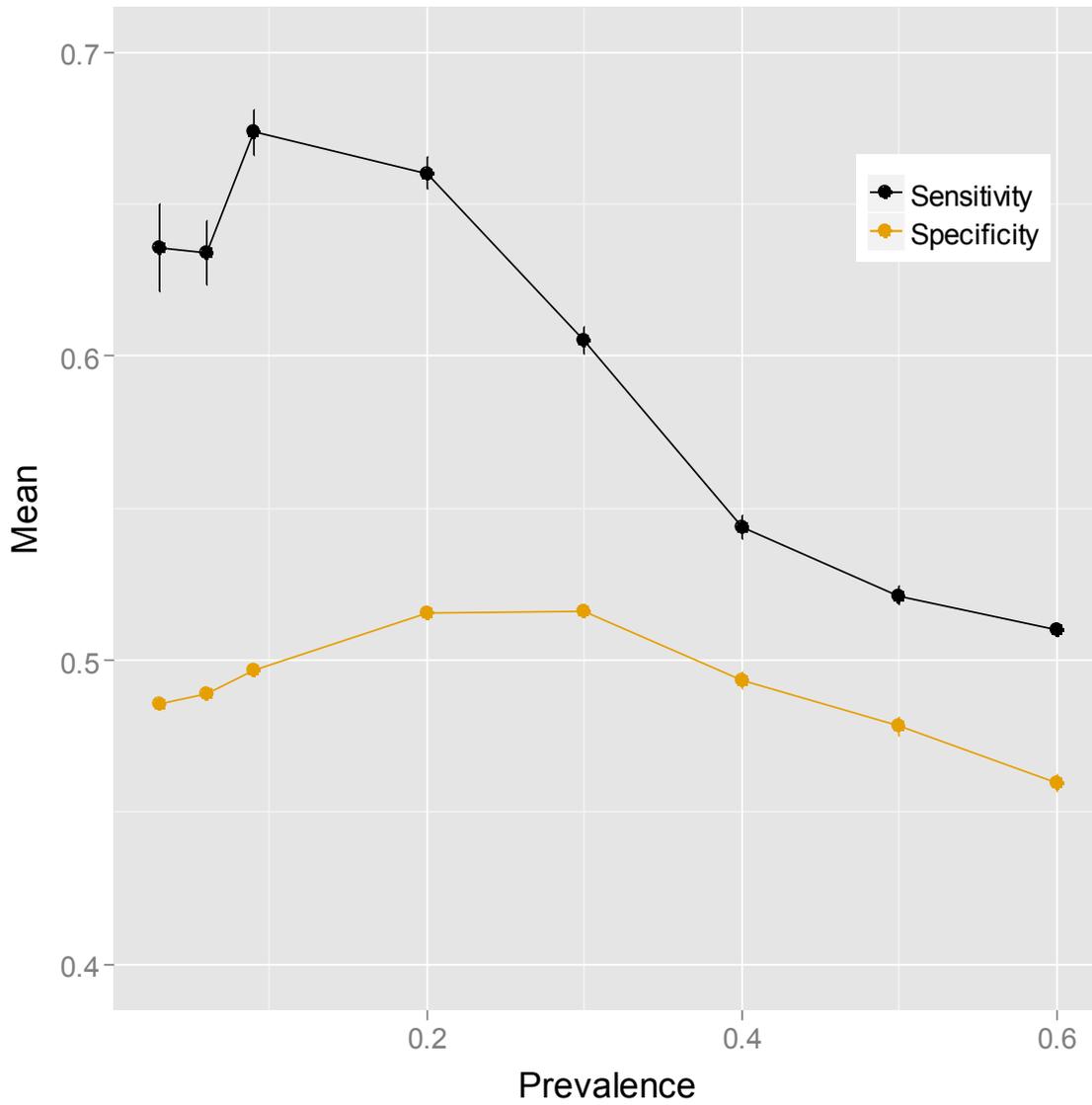


Figure 3.3: Model performance (AUC) with confidence intervals showing the results from different years, at different prevalence levels, pooled by A) the 5 different prevalence levels; and B) the 3 years of independent data plus all the years combined.



*Figure 3.4: Average (across all thresholds) specificity (true positive rate) and sensitivity (true negative rate) with confidence intervals for each prevalence level for 100 samples of 500 observations evaluating the GLM2 model against the aggregated remote sensing data.*

## **Chapter 4 - How sea otter (*Enhydra lutris*) recovery is changing the social-ecological landscape in Pacific Canada**

An understanding of trade-offs is central to decision making in the context of ecosystem-based management (EBM). Accordingly, regional scale assessments of ecosystem services trade-offs are becoming increasingly common (e.g., Guerry et al. 2012, Nelson et al. 2009, White et al. 2012). However, the complexities of social-ecological systems require many simplifying assumptions before any such system can be represented. With the continued emphasis on monetary values, the ecosystem services literature has focused on economic valuation of services (Bagstad et al. 2013), often at the expense of a realistic representation of the underlying social-ecological system (Norgaard 2010). In contrast, ecosystem models include considerable ecological complexity, and a wide range of indicators have been proposed for fisheries (e.g., Cury and Christensen 2005, Fulton et al. 2004), ecosystem health (Vandermeulen and Cobb 2004), and biodiversity (Levin and Lubchenco 2008, Zacharias and Roff 2000). However calibrating these indicators with empirical data (Rombouts et al. 2013) and articulating them for management (Shin et al. 2010, Shin and Shannon 2010) remain significant challenges.

These challenges reflect the complexity of translating indicators of ecosystem state into the values managers must regularly trade-off to make decisions. Three areas of advances are necessary before credible regional forecasts of salient values are available to decision makers. First, analyses of social-ecological systems will need to integrate local data with sophisticated models with enough complexity to reasonably represent the social-ecological system (Norgaard 2010). Second, management actions should be linked through ecosystem models to benefits and values (Granek et al. 2010, Tallis et al. 2012). Third, useful and transparent representations of uncertainty are crucial but lacking (Ruckelshaus et al. 2015). In this study we offer advances in all three aspects.

These advances allow us to answer a crucial question of a famous ecological story: what are the broader regional implications of the sea-otter return? The trophic cascade induced by re-introduced sea otters (*Enhydra lutris*) in nearshore ecosystems has been well studied since the

1970s, and is broadly seen as an ecological success story (e.g., Estes and Palmisano 1974, Watson and Estes 2011). However, the sea otter is also seen as a formidable competitor for resources, particularly commercial invertebrates. Thus, the transition from an invertebrate-dominated to a kelp-dominated ecosystem has led to conflict with established invertebrate fisheries (e.g., urchin, geoduck, crab) and coastal communities dependent on these fisheries. While the potential for conflict was anticipated (e.g., Johnson 1982, Watson and Smith 1996), and anecdotal reports of reduced catch are regularly reported by fishers, no quantitative assessment of regional costs and benefits has yet been attempted (though see Loomis 2005).

We take advantage of the natural experiment underway on the west coast of Vancouver Island (WCVI), British Columbia, to quantitatively assess the change in four ecosystem services as an otter-absent system transitions to an otter-present one. Using an ecosystem model calibrated with purpose-collected, local data, we provide the first quantitative, multi-value analysis of the sea otter-induced trophic cascade, including a reasonable treatment of the associated uncertainties. The case study illustrates how local studies can be scaled to regional models with sufficient ecological complexity to reasonably estimate salient benefits, along with a defensible and comprehensible estimate of model uncertainty. Using data collected in areas where sea otters are at carrying capacity and where they are absent, we modelled the trophic cascade from an otter-absent to an otter-present system using the Ecopath with Ecosim (EwE) software (Christensen and Walters 2005). We created a balanced Ecopath model representing the otter-absent system (1970). Then, using space-for-time substitution, we parameterised the temporal dynamics (Ecosim) according to observed, proportional changes in biomass to predict an otter-present state. Our study area included hard and soft bottom habitats to 50 m depth, the practical limit for sea otter foraging (Bodkin et al. 2004). We focused the trophic model on the main prey species in the sea otter diet, and on species assemblages (functional groups) associated with rocky reef ecosystems.

We compared the two systems using the landed value of the catch, and the predicted economic contribution of carbon sequestration, nutritional supplement, and tourism. We expressed all values in 2015 Canadian dollars, with no discounting. To assess trade-offs in ecosystem services

we first consider the economic costs to fisheries, and then describe how increased production in the kelp-dominated system provides a fisheries benefit by translating surplus production into commercial fisheries biomass not explicitly represented in the model. We also estimate the economic benefits of carbon sequestration and tourism before describing a number of less quantifiable ecological and cultural services provided by an otter-present system, thereby illustrating how a more comprehensive assessment of ecosystem state can broaden the decision making context and facilitate management decisions.

We addressed model uncertainty at two levels, within the ecosystem model and in the translation of indicators to benefits. Within the Ecosim model, we tested how randomising the input parameters to the 1970 model influenced the resulting 2050 prediction. We estimated the confidence in the resulting benefits by re-sampling (usually based on empirical error distributions) the variables (e.g., \$ per tonne, carbon content) used to translate biomass into each service considered.

## ***Methods***

### **Ecosystem model**

We based the ecological scope of our ecosystem model on sea otters and their prey. We included the commercial species explicitly, and grouped non-commercial species into functional groups, a common practice in ecosystem models. We collected available data on species density (B), production (P/B) and consumption (Q/B) rates, and diet composition. Data availability was variable, with commercial species typically being better studied.

In addition to collecting available data, there was also the matter of scaling the data to the study area. Since abundance data are typically conducted 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 scale the density correctly. This is a critical challenge facing the translation of local field data to management-relevant models.

Our study area encompassed the central portion of the West Coast Vancouver Island (WCVI), extending from Brooks Peninsula in the North to Pachena Point in the South (Fig. 1.1). We

included waters from the low water line to 50 m depth, the range of potential sea otter foraging.

We obtained estimates of B for the 1970 model from various sources, including longitudinal field data from the Kyuquot region where otters were introduced (Watson and Estes 2011), and from Barkley Sound which otters are yet to occupy. Biomass for some commercial species was available from fisheries data, while B for other groups, especially lower trophic levels, needed to be estimated indirectly. Diet composition, and production and consumption rates were obtained from a variety of sources detailed in Appendix 1.

Data from local field studies need to be scaled to the study area as Ecopath uses average biomass across the area of interest. To scale data collected in either rocky reef or soft-bottom habitats we used Gregr et al.'s (2008) estimate that 30% of the area is rocky reef. We further assumed that 10% is suitable for infaunal organisms and that depths are uniformly distributed between 0 and 50 m.

We classified the quality of the data for each group using three levels (Table A.9), assigning High to parameters derived from data collected in the study area, and for which the habitat proportion could be reliably scaled. We assigned Medium to those B values 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, the data were ranked solely on perceived quality. We used this information to parameterise the Monte Carlo parameter simulation.

### **Ecosystem dynamics**

Sea otters are effective at limiting populations of benthic invertebrates, most notably sea urchins, clams, abalone, large crabs, and mussels (Riedman and Estes 1990). When abundant, sea urchins are consumed preferentially, likely because of ease of capture. As urchin abundance is reduced, sea otter diet diversifies to include bivalves, snails, chitons, crabs, sea stars, and in some cases even fish (Estes et al. 1978). In soft sediment habitats sea otters often excavate a range of bivalve prey including butter clams, horse clams and geoducks (Kvitek et al. 1993).

In the eastern North Pacific, sea otters preferentially eat sea urchins when re-colonising an area, releasing brown kelps from predation pressure and often triggering a trophic cascade resulting in a kelp-dominated ecosystem (Estes and Palmisano 1974, Watson and Estes 2011). Representing this dynamic was an explicit objective of the model configuration.

Ecosim represents ecosystem dynamics using a number of observed phenomena that are difficult to parameterise. 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). We used a time-series fitting routine to parameterise vulnerabilities by minimising the difference between the model predictions and estimated population trends. This was facilitated by grouping the sea otter prey into 3 ecologically-based vulnerability classes (Table A.8). To represent the increase in rockfish habitat due to kelp, we used a standard mediation curve (Harvey and Rose 2014).

### **Ecosystem service valuation**

*Existing fisheries:* This service is comprised of 5 established commercial species (red sea urchin, large crab, geoduck clam, other edible clams, and lingcod) closely associated with the modelled ecosystem. The difference between the two states was measured using the change in annual landed value of the catch. Randomised catch from each period was multiplied by landed values sampled from a normal value distribution with a mean and standard deviation calculated from 10 years (2001-2010) of regional catch data (Province of British Columbia 2014). Landed values were converted to 2015 dollars using the Canadian consumer price index (Canada 2016). After multiplying the catch by the landed value, the difference between the two periods represents the change in annual value, in 2015 Canadian dollars, of existing fisheries.

*Supplemented catch:* We assumed a portion of the biomass not accounted for in the model (i.e., model surplus) was available for consumption by higher trophic levels (HTLs), thus providing a nutritional supplement to HTL finfish. Annual model surplus is defined as the biomass produced but not consumed each year by the groups explicitly represented in the model.

We estimated the biomass of this supplemented catch using trophic transfer efficiencies (TTE) to convert the fate of unaccounted for biomass at different trophic levels to HTL commercial

finfish species. We divided the model groups into 3 trophic levels, and for each level estimated how much B would be transferred to the HTL finfish using randomised values for TTE. We defined the trophic levels (primary production, secondary production, and forage fish) to be 1, 2, and 3 trophic steps away from the valued finfish. TTEs were randomised using truncated (at 0) normal distributions parameterised ( $\mu = 0.10$ ,  $SD = 0.58$ ) according to Pauly et al. (1995) for the carnivorous trophic transfers and Ware (2000) for the herbivorous (primary to secondary production) transfer ( $\mu = 0.25$ ,  $SD = 0.1.16$ ). Surplus biomass from each trophic level was then transformed into HTL finfish biomass based on its trophic distance. For example, primary production was transferred across 3 levels, while forage fish were transferred across only one. The annual landed value (\$/tonne) of the supplemented catch was drawn from a triangular distribution using a peak = 2.77, the weighted, average landed value of the main nearshore commercial finfish groups (salmon, lingcod, rockfish, and halibut), and a range from 1.74 to 8.53, the minimum (rockfish) and maximum (halibut) average values (Province of British Columbia 2014). Average annual landed values from 2001 to 2010 were used, after converting to 2015 dollars using the Consumer Price Index (Canada 2016).

The uncertainty in the predicted annual value of the nutritional supplement is a function of myriad social-ecological processes, including species interactions across a range of space and time scales, and the vagaries of the over-arching social system. We sought to reflect this uncertainty by randomising the surplus biomass available to the food web, the TTEs, and the value of the HTL finfish.

*Carbon sequestration:* The kelp available for sequestration was scaled to total carbon using values for % dry and % carbon from Wilmers et al. (2012). We calculated net annual primary production (NPP) using the species-specific P/B and ecotrophic efficiency values from the Ecopath model. The proportion of kelp detritus fluxed to the deep ocean was estimated by sampling from a triangular distribution parameterised with the range of values (0.01 to 0.5) proposed by Wilmers et al. (2012). Finally, the dollar amount was drawn from a normal distribution with mean and standard deviation based on the mean annual carbon price from the California Carbon Exchange (CPI 2016). These parameters were calculated using daily data

on carbon price and exchange rate from September 2011 to December 2015, and converted to 2015 dollars.

*Tourism:* We based our estimate of increased tourism revenue on a recent survey of Vancouver Island visitors (Martone, unpublished data), which found willingness-to-pay for a nature tour increased by an average of \$227.75 per visitor (2015 Canadian dollars) if the trip had a very high vs. a low chance of seeing sea otters. We sampled this per visitor value using a normal distribution with a standard deviation = 53.37, estimated from a model of the underlying willingness-to-pay parameters (Martone et al., unpublished data; Frishman 1971). We estimated the total number of visitors by sampling from a normal distribution using the average and standard deviation from 10 years of visitation data to a national park within the study area. Martone et al. found that 27.6% of visitors planned on engaging in wildlife tours.

### **Uncertainty characterisation**

We explored the parametric uncertainty in both the ecosystem model itself, and in the calculation of the four ecosystem service values. First, we randomised a subset of ecosystem model parameters, repeatedly sampling biomass, production and consumption rates, and diet proportions from normal distributions centred on the balanced values, with standard deviations estimated according to assumed data quality. The randomisation was repeated until a sample of 1000 balanced models was obtained. The randomised, balanced models were run through Ecosim to generate 1000 alternate future scenarios. The resulting paired biomass values from the otter-absent and otter-present models represent the variability in biomass of the ecosystem service providers on which the ecosystem service calculations are based.

For each ecosystem service, we added additional uncertainty in the transformation of B to present dollar value. Our estimates of the value of commercial catch included uncertainties representing variability in catch and landed value. For secondary production, we included the additional uncertainty around trophic transfer efficiency and pathways. Our estimate of the value of carbon sequestration included uncertainty around the flux of biomass to deep water, the total carbon content of primary producers, and the price of carbon. Finally, we represented

uncertainty in the tourism value of sea otters using the range of values obtained from surveyed, willingness-to-pay data and measured variability in the annual number of visitors.

### ***Results and discussion***

The model captures the trophic cascade well, reproducing the observed decline of commercial invertebrate species, including geoduck clam, large crabs, and sea urchins within the study area (Fig. 4.1). It also predicted increases in kelp abundance and a variety of finfish and invertebrate species (Fig. 4.2). The total change in aggregate predicted biomass (+37%) reflects the changes observed between otter-absent and otter-present sites for most groups. All predicted values are reported as median [5th percentile, 95th percentile].

We estimated the economic loss to commercial invertebrate fisheries at 6.67 [4.29, 9.49] M\$/year (Table 4.1). A decline in geoduck catch of 25% comprised over half of this cost. The remainder included the predicted loss of the commercial crab and sea urchin fisheries, and a 28% reduction in the clam fishery. These costs are partially offset by a notable increase in the catch of lingcod (Table 4.2, Fig. 4.1). On the WCVI, the impact of otter predation on the geoduck fishery has been more dramatic than these numbers suggest - as of 2012, 33% of the commercial beds have been closed due to sea otter impacts (compared to 11% coastwide) (DFO 2012). In contrast, data from SE Alaska show that while sea otters do prey on the largest individuals, sizeable populations remain. This corresponds with other recent work on the WCVI that failed to detect a difference in abundance between otter-occupied and otter-absent areas (Reidy and Cox 2012). Collectively, this evidence suggests that sea otter impacts on geoduck beds may be quite site-specific. As for the large crab (primarily Dungeness), while they largely disappear from the modelled system, in reality their habitat extends well below the foraging depth of sea otters. Thus, while lucrative crab fishing grounds in shallow waters may well be lost, large crabs are unlikely to be extirpated by sea otters.

More generally, historic patterns in fisheries data suggest the relationship between reduced biomass and lost revenue is not linear, with reductions in biomass of high value species often leading to an increase in price and higher overall revenue to fishers (though for a particular region in a global context, this may lead to loss of market share). Thus, a decrease in geoduck

and large crab biomass and more expensive fishing practices may well lead to higher prices, further mitigating the economic impact.

Any potential impact of sea otters on invertebrate fisheries must also consider the impacts of the fisheries themselves, as this can be conflated with sea otter effects. This is particularly true for fisheries developed in the same decade sea otters were re-introduced. For example, the sea urchin fishery began in the early 1970s (Campbell et al. 2001), and geoduck fishing began in 1976 (DFO 2012). Most egregious is the abalone fishery which began in earnest in 1972 but was permanently closed in 1990 (Campbell 2000) through no fault of the sea otter.

The higher productivity of the otter-present system is due primarily to an increase in kelp and small grazing invertebrates (Fig. 4.1, Table 4.3). The portion of this increased production that is not explicitly consumed in the model provides a supporting service to higher trophic levels. We estimated this nutritional supplement to be worth 11.65 [2.98, 39.00] M\$/year, of which 67% was attributable to kelp and 32% to the invertebrate groups. Uncertainties are high for this service because the parameters describing the fate of the kelp detritus, the TTEs, and the ultimate landed value, are unknown. Nevertheless, the contribution of kelp detritus to the food web is significant. The estimated value to the overall economy is considered conservative because the value from up- and down-stream economic impacts, other lucrative ecosystem services (e.g., sports fishing), and the wider set of supporting services have not been included.

A portion of the unconsumed, increased biological production will also contribute to carbon sequestered in the deep ocean. Our model predicted a net benefit of 0.63 [0.16, 1.75] M\$/year for the sequestered carbon based on randomised deep ocean flux and California carbon prices. This is less than 1/10 of the 8.02 M\$/year obtained by scaling comparable results from Wilmers et al. (2012) to our study area. This difference is attributed to a number of factors including more conservative scaling of kelp habitat, consideration of density dependence, and variable production and ecotrophic efficiency rates for different groups of laminariales (i.e., brown kelps).

Tourism is predicted to benefit most from the sea otter recovery. Our analysis suggests that an otter-dominated system will generate 48.39 [29.42, 67.77] M\$/year in additional tourism

revenue based on willingness-to-pay data (Martone et al. unpublished data) and historic visitation rates. This system would also increase other tourism-related services not explicitly valued here such as recreational fishing (due to more abundant nearshore finfish) and destination dive tours. Conversely, the recreational crab fishery will likely experience a loss in value because of reduced accessibility. However, the depth refuge of large crab may make this a marginal loss only, as many recreational fishers—as with the commercial fishers discussed above—may adapt to this presumed shift to deeper waters.

Although the four services described above are the most monetisable, it is less clear that they are the most important. The social and cultural values associated with increases in catchable biomass of nearshore fishes are multiple and important (Klain and Chan 2012). In addition to providing important provisioning services to coastal communities, such subsistence catch is often bundled with social values such as belonging, independence, and sense of place (Klain and Chan 2012). Maintaining sense of place is especially important in a generational sense, as young people often see little future in coastal communities where opportunities are limited. In the face of declining salmon abundance, First Nations on the WCVI are increasingly relying on the kelp-associated black rockfish to serve as a gateway fish to help young community members engage in this part of their culture (Chan et al. 2012). This redistribution of biomass from commercial invertebrates to nearshore fish species can, depending on values, represent a more equitable distribution of the region's marine resources, particularly since the highly consolidated commercial fisheries provide limited to no return to coastal communities on WCVI (Klain and Chan 2012).

Finally, we consider the supporting services provided by the WCVI to the health and productivity of the broader ocean. As an exposed, dynamic coastline, our study area is perhaps the antithesis of a closed system. This dynamic environment encourages a constant exchange of both plankton and nekton with deeper waters, supporting our assumption that much of the surplus production remains biologically available. This surplus undoubtedly provides valuable supporting services, and our study quantifies the potential size of this contribution.

Of seven regions in the eastern North Pacific, the WCVI was found to be the second most productive with net primary productivity (NPP) estimates of 406 and 524 g C m<sup>-2</sup> year<sup>-1</sup> (Perry and Schweigert 2008). Importantly, Perry and Schweigert (2008) did not consider the contribution of kelp forests, which, through detritus, are estimated to contribute as much as 40% to the biomass of benthic invertebrates and rockfish (Ramshaw 2012). Ware and Thomson (2005) showed that the BC shelf exports considerable biomass of commercial species to the rest of the eastern North Pacific. However, they noted that their estimated NPP from pelagic plankton production of 153 - 369 g C m<sup>-2</sup> was insufficient to support the fisheries biomasses observed. Coastal kelp systems are the obvious source of that additional biomass, implying that they provide 25-60% as much primary production as a temperate upwelling zone. Kelp-dominated nearshore areas like the WCVI likely serve as valuable nutrient pumps, making them more significant to the world's oceans than previously described (e.g., Agardy et al. 2005).

The importance of such nutrient pumps to other coastal species is also likely high. Many predatory fishes, birds, and marine mammals rely on nearshore ecosystems, and the nutritional supplement provided by kelp in the otter-dominated system undoubtedly benefits a range of higher trophic levels, and other ecosystems. Many species, including high value commercial fish, also use kelp forests as habitat during early life history stages. While this effect, one of several mediation effects of kelp on nearshore species (Markel 2006), still needs to be fully quantified, kelp forests do represent a class of ecosystems that has been proposed to enhance biodiversity and community composition (Bode et al. 2011).

### **Model performance and uncertainty**

The model successfully reproduced the key features of the trophic cascade, capturing the reduction of grazers by sea otters, and the subsequent recovery of kelp forests. Several ecological phenomena were necessary to emulate the trophic cascade. First, the ecotrophic efficiencies (Christensen et al. 2008) of the kelp groups needed to be very high to allow recovery when released from grazing pressure. Second, sea otter prey biomasses had to be at levels that allowed some serial depletion, otherwise all prey were simply reduced to lower abundance. Vulnerability (sensitivity to top-down changes in carrying capacity) was also key to

triggering the trophic cascade (see Appendix 1). Other parameters with potential effects that were not further explored include the amount of detritus retained in the model (relevant to carbon sequestration and nutritional supplement) and mediation (a value with a notable effect on finfish production). Changes in all these parameters had notable effects on the model dynamics, and often led to results predicting even greater increases in biomass in the otter-present state. However, since these parameters are difficult to estimate from data, we used values that ensured conservative estimates of biomass change between the two systems.

### **Confidence**

Confidence in model results is typically based on agreement with other observations, and on the robustness of the model to variability in input parameters. Observed changes in biomass (based on space-for-time substitution) for several key species (kelp, geoduck clam, large and small grazers) were well represented by the model predictions, although others (mussels, predatory invertebrates, mesograzers and sessile invertebrates) were not, suggesting the possibility of an incomplete food web. The sea otter diet at equilibrium was similar to that observed in otter-occupied areas elsewhere (Honka 2014, Laidre and Jameson 2006). Thus, although some observations were not represented by the model (perhaps due to scaling, structural, or sampling errors), it nevertheless faithfully reproduced the main components of the otter-present and otter-absent nearshore ecosystems. This sort of mixed performance, where some aspects are well represented and other not, has been observed in other ecosystem models (e.g., Cox and Kitchell 2004) and may well be correlated with model complexity.

We tested the robustness of the ecological portion of the model by randomising the base and diet parameters of the starting (1970) Ecosim state. The confidence intervals around the resulting B estimates (Fig. 4.1) confirmed the model was robust to these parameters. We suggest that situations where structural uncertainty dominates parametric uncertainty (e.g., Wood and Thomas 1999) may also be related to model complexity, as our experience shows how increasing model complexity reduces the range of potential parameter values.

For the benefit functions, we had no observations with which to parameterise or evaluate their performance. We therefore took the approach that our uncertainties should be wide enough

that making them wider would seem unreasonable. The intent is to represent the (unknowable) uncertainty about the social-ecological context where the scenario valuation will actually unfold in a way that will allow relative comparisons to be robust to those uncertainties. Despite the combination of parametric uncertainty in the ecosystem model and the intentionally broad uncertainty estimates for the benefit calculation, the differences between the two ecosystem states were large and significant.

Models of social-ecological systems require myriad assumptions about social and ecological parameters and processes. It is impossible to accurately represent all the uncertainty these assumptions contain. To overcome this challenge, our approach of predicting benefits with wide distributions illustrates how we can begin to examine uncertainty in an integrated sense. Hypothesising the maximum reasonable uncertainties for the assumptions required to translate biomass into services provides a more holistic characterisation of the overall uncertainty in the final benefits prediction. It also effectively bundles the uncertainties contained in the social or ecological details underlying the assumptions, making them more amenable to further investigation. We argue that partitioning uncertainties in this top-down fashion is an important first step in understanding and analysing the overall uncertainties in ecosystem models. Such integration and presentation of uncertainties, particularly across a suite of ecosystem services (e.g., Fig. 4.3), provides important information on the confidence we should have in the results, potentially making them more relevant to management.

### ***Conclusions***

Changes to ecosystem services are a globally relevant topic. Forecasts from ecosystem models are essential for supporting ecosystem-based management at both short-term political, and long-term generational time scales. Our analysis highlights the importance of examining ecological change holistically: valuing a broader set of services allows comparisons that are more salient to stakeholders and places less emphasis on accurately estimating marginal economic changes.

Based on our analysis, costs to existing invertebrate fisheries from sea otter re-occupation of the WCVI would be more than offset by the increased productivity of the kelp-dominated

system. The projected loss to invertebrate fisheries is about half the value of the predicted nutritional supplement. The greatest benefits are predicted to accrue from tourism.

While sea urchins face possible economic extirpation, impacts on other lucrative invertebrate fisheries (crab, geoduck) may be smaller than anticipated given the ecological, social, and economic factors that may mitigate the impact. The 37% increase in overall productivity due to coastal kelp systems contributes a regional supplement that may be as much as 60% of what is produced by oceanic phytoplankton in the WCVI coastal region. This emphasises the role of the WCVI as a net exporter of biological productivity, effectively acting as a nutrient pump in the eastern North Pacific, and highlights the potential importance of kelp forests globally.

We also identified a number of less fungible social and cultural benefits that would likely accrue to coastal communities from a more productive nearshore ecosystem. These include a more resilient social-ecosystem due to increased ecological redundancy, increased equity in resource distribution, and an enhanced connection to place from increased nearshore fishing opportunities.

The dominance of the parametric uncertainty in the benefits model over the uncertainty in the ecosystem model parameterisation emphasises the importance of explicitly estimating uncertainties in the high level assumptions required by the benefits model. Bundling the underlying, more detailed uncertainties in this way both captures the knowledge needed for the benefit prediction, and sets the stage for model detailed investigations of uncertainty. This rather intuitive approach to formalising assumptions refines our understanding of both the system, and the limits of our understanding.

This work illustrates how adopting a broader, more diverse perspective can, despite high uncertainty, offer more information about the outcomes of different management strategies. This has important implications for management, as it allows resource managers to see a bigger picture, enabling expanded set of management options, and clearer, more equitable decisions with increased confidence.

*Table 4.1: Median change in value (millions of 2015 Canadian \$) 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 uncertainty from randomisation tests, shown as the 5th and 95th percentiles.*

<b>Service</b>	<b>5th %</b>	<b>Median</b>	<b>95th %</b>
Commercial catch	-9.49	-6.67	-4.29
Secondary production	2.98	11.65	39.00
Carbon sequestration	0.16	0.63	1.75
Tourism	29.42	48.39	67.77

*Table 4.2: Change (from 1970, otter-absent to 2050, otter-present) in annual landed value (millions of 2015 Canadian \$) of nearshore commercial species on the West coast of Vancouver Island based on median landings (in kilo tonnes)*

	<b>Landings (kt)</b>		<b>M\$/kt</b>	<b>Annual Value (M\$)</b>		<b>Δ (M\$)</b>
	<b>1970</b>	<b>2050</b>		<b>1970</b>	<b>2050</b>	
Sea urchin	0.20	3.4E-04	4.28	0.86	0.00	-0.86
Commercial crab	0.25	4.8E-09	6.54	1.63	0.00	-1.63
Geoduck	0.81	0.61	22.86	18.43	13.95	-4.49
Other edible clams	0.30	0.22	3.36	1.00	0.72	-0.28
Lingcod	0.12	0.36	2.25	0.28	0.81	0.53
				22.21	15.48	-6.73

Table 4.3: Biomass values ( $g\ m^{-2}$ ) for the baseline 1970 model (B-start) and the mean (un-randomised) 2050 model (B-end) with the relative change in biomass (E/S) by model group.

<b>Group name</b>	<b>B-start</b>	<b>B- end</b>	<b>E/S</b>
Sea otter	4.76E-04	0.04	93.79
Urchin	29.04	0.05	1.60E-03
Large commercial crab	0.07	1.49E-09	2.28E-08
Geoduck	70.01	52.76	0.75
Mussel	82.66	68.41	0.83
Other edible clams	19.40	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 crab	0.87	3.17	3.62
Predatory inverts	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 inverts	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
Nereocystis	14.94	18.22	1.22
Macrocystis	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
<b>Total</b>	<b>335.57</b>	<b>460.90</b>	<b>1.37</b>

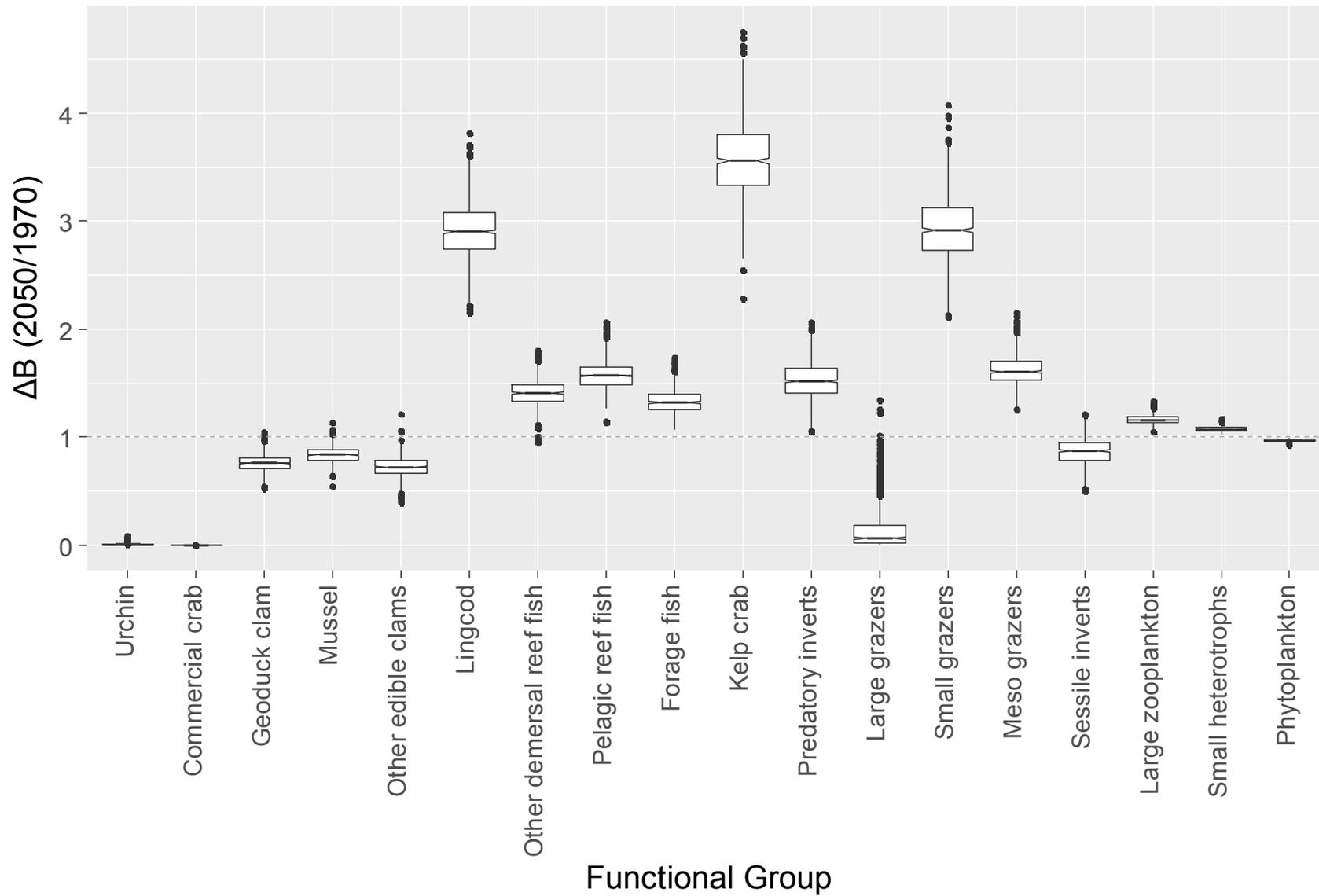


Figure 4.1: Relative change in biomass ( $\Delta B$ ) for main functional groups.

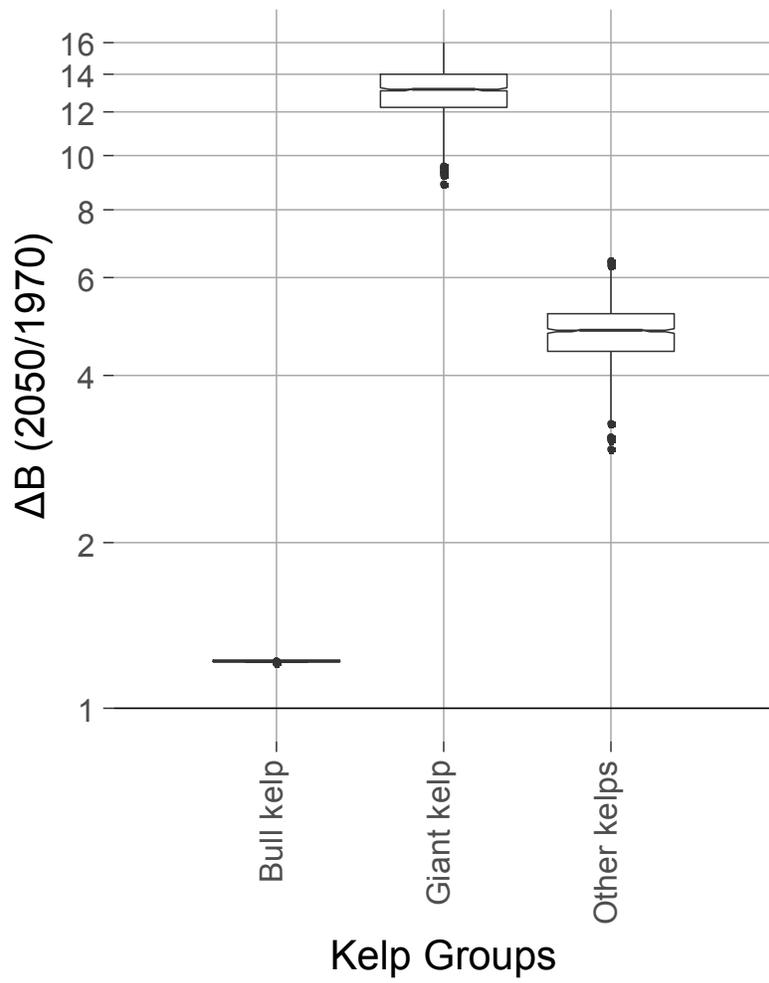


Figure 4.2: Relative change in biomass ( $\Delta B$ ) for the kelp groups.

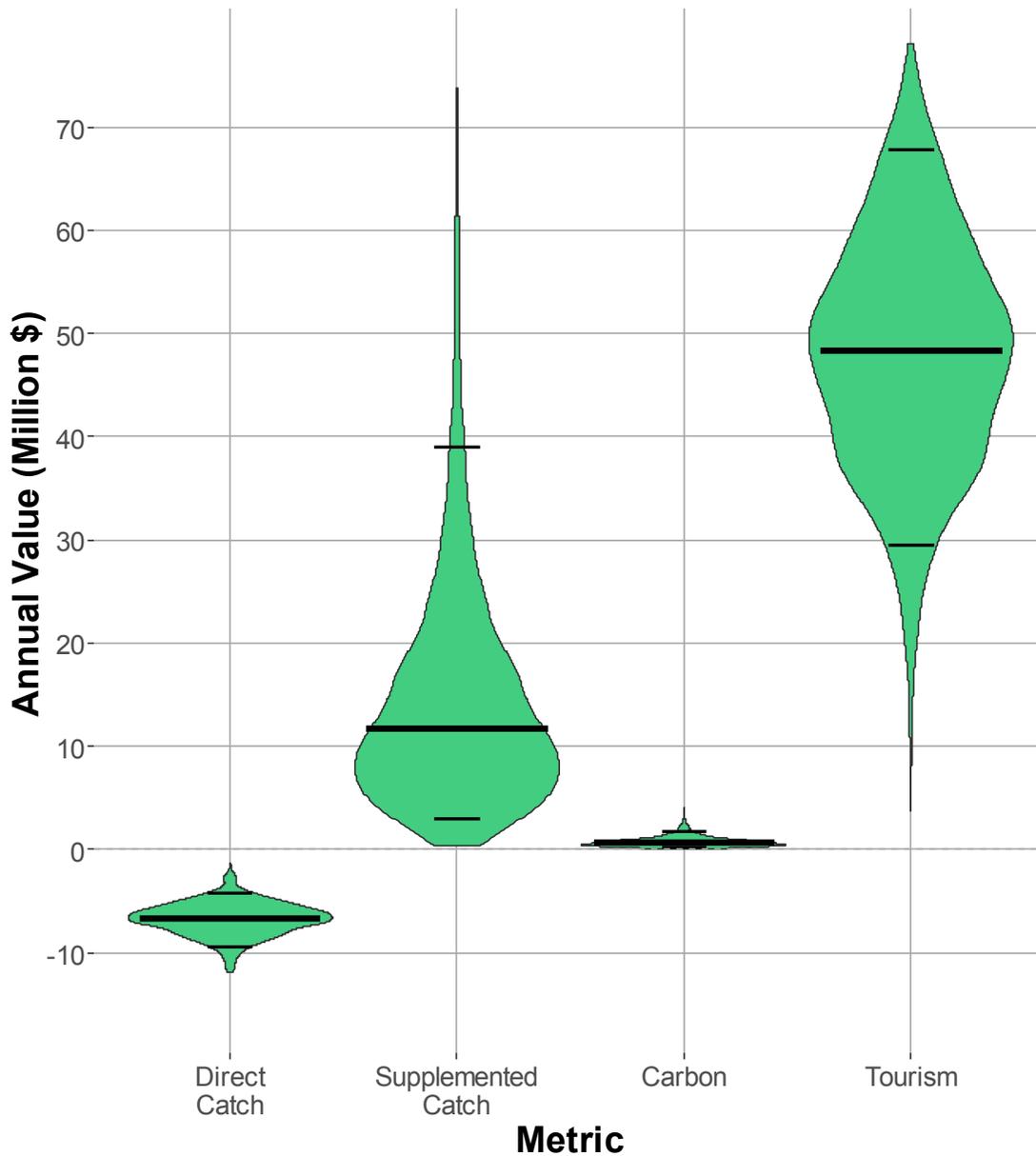


Figure 4.3: Sea otter-induced change in annual value for 4 ecosystem services represented as difference in 2015 Canadian dollars between an otter-absent and otter-dominated ecosystem on the West Coast of Vancouver Island. Shown as violin plots where the relative width of the plot represents the distribution of the prediction (like a histogram). The mean, 5th, and 95th percentile are show as horizontal lines. The randomised credibility interval are comprised of explicit uncertainties related to the translation of ecosystem service supply to dollar values.

## **Chapter 5 - Pushing the envelope: How mapping marine ecosystem services enhances equitable ecosystem management**

The benefits humans derive from ecosystems are increasingly valued through the lens of ecosystem services. A comprehensive representation of the services valued by stakeholders is central to meeting the challenge of ecosystem-based management. To date, however, such management advice has come largely from either (1) aspatial population models representing nonlinear species interactions, or (2) spatially explicit models of service provision that deny complex ecosystem interactions. The first cannot represent place-based benefits (e.g., resource access), while the latter cannot represent non-marginal ecosystem change. This chapter presents an integrated modelling approach that explicitly integrates (1) with space using predictions of realised habitat for key species (i.e., service providers) before applying a benefits model to forecast a suite of consumptive and non-consumptive benefits. We develop our model for the sea otter-kelp system in coastal British Columbia, Canada and evaluate how the benefits respond to three spatially explicit sea otter management alternatives.

Marine resource management continues to evolve away from an approach that treats resource sectors independently towards approaches that consider both the interactions between sectors, and the complicating effects of a dynamic, uncertain marine environment. Integrated, or ecosystem-based management (EBM), rooted in the understanding that ecosystem components do not function independently, has long been seen as the appropriate framework for ensuring the sustainable flow of goods and services while also managing human impacts on natural systems and balancing diverse stakeholder values (Grumbine 1994, Slocumbe 1998).

The characterisation of natural systems as the source of ecosystem services (ES) has emerged as a useful way to articulate the links between ecosystems and stakeholder values (Tallis et al. 2010), providing an intuitive way to translate the diversity of natural resources into valued benefits. However, because neither stakeholder values, nor the ES production to which they relate, are uniformly distributed, spatial resolution is essential to the appropriate evaluation of management alternatives.

Ecosystem models are essential to such efforts for a variety of reasons, including the ability to forecast ecosystem service supply and distribution. However, models focused on supply have been criticised as being over-simplified and lacking ecological sophistication (Norgaard 2010), although more sophisticated ecosystem models can be difficult to spatialise. For example, the spatial component (Ecospace) of the most widely used ecosystem modelling tool (Ecopath with Ecosim) represents less than 7% of the models constructed to date (Coll  ter et al. 2015), at least partially due to the challenges of parameterisation (Romagnoni et al. 2015). This speaks directly to the many known unknowns in the spatial ecology of marine systems. Others have noted a disconnect between management actions and associated ecosystem impacts (Granek et al. 2010), and the patchy treatment of uncertainty (Gregr and Chan 2014).

Further, the relevance of EBM critically depends on how the benefits derived from ecosystem services are represented. Equating benefits with service supply invokes the fallacy of trickle-down benefits (Wieland et al. 2016) - ignoring the technical, social, and governance barriers that can affect stakeholders' realisation of benefits. Realising the benefits of increased service production can depend on infrastructure (e.g., tourism and sports fishing), or simply the proximity of the service provision to communities (e.g., subsistence). While some stakeholders (e.g., large commercial operations) or services (e.g., clean air) may be unaffected by access, it is likely that when service supply is geographically patchy, stakeholder access will be uneven.

Equity issues arise when benefits are not equally accessible to all stakeholders, or when benefits are not legitimately represented. To support our discussion of equity and other social benefits, we adopt the concepts of credibility, legitimacy, and salience (Cash et al. 2003) as indicators of the overall utility of an analysis to an EBM context. Credibility refers to the soundness of the science, also perceived as the uncertainty; legitimacy refers to the appropriate representation of stakeholder values, and salience to the relevance of the management alternatives to decision makers. Without including benefits that are meaningful to stakeholders, analyses of alternatives can lose legitimacy. If EBM is to be equitable, it must consider both service production and the realisation of benefits across stakeholders. This more

nuanced understanding of how benefits are resolved will also help decision makers construct more salient management alternatives by including well resolved, spatially explicit, benefits.

Spatially resolving benefits depends on understanding current distributions of valued species. It also requires a reasonable representation of the social-ecological system, including how management actions influence their abundance and distribution, and how this may change in the future. Such distributions are typically grounded in habitat suitability models, and forecasts from such models are now seen as central to integrated management (e.g., Guerry et al. 2012).

Of course, what is reasonable depends on model objectives (Gregg and Chan 2014). Distribution models supporting long-term, policy-driven questions (e.g., Halpern et al. 2008, Millenium Ecosystem Assessment 2003) generally require less resolution than those designed to support more immediate, tactical management questions (e.g., harvest rates; protected area designation). Such strategic models will typically be well served by models of potential distributions (e.g., Cheung et al. 2008), while tactical models will require more realistic representations of biomass and its distribution across the species' realised habitats (sensu Hutchinson 1978). Our interest here is the active management of sea otter distributions, a tactical question that depends on the realised distributions of the ES providers.

Mapping the distribution of ES provider biomass is the first step in measuring accessible benefits as this underpins virtually all ecosystem services. Such maps are also valuable because for many stakeholders the connection with ecosystem services is through the abundance and distribution of these species. Understanding these distributions thus helps ground stakeholders before service provision becomes abstracted to benefits. In this way, species distribution maps provide an effective snapshot of the full bundle of services. Applying management actions to these spatial distributions then clearly couples action and impact, further grounding the analysis.

By linking population dynamics, habitat suitability and benefit models we illustrate a number of technical advances in ecosystem modelling. We also show how indicators for non-fungible benefits can emerge when the distribution of benefits are appropriately resolved, and how such benefits respond to different, spatially explicit management scenarios.

The context for this work is provided by the trophic cascade commonly observed in sea otter–kelp coastal ecosystems (Estes and Duggins 1995, Paine 1980). Throughout the eastern North Pacific sea otters are re-occupying habitat from which they were extirpated during the fur seal hunt of the 18th and 19th centuries. Although this recovery represents an important ecological success story, the expanding sea otter population is often seen as a threat to a number of established invertebrate fisheries.

On the west coast of Vancouver Island, British Columbia, Canada (Fig. 5.1), a series of re-introductions in the 1970s led to a small population of otters, which has since reached carrying capacity in Kyuquot and Nootka Sounds, and is poised to extend its range across the remainder of the island (Nichol et al. 2009). The inevitable and on-going fisheries conflict was anticipated almost half a century ago in Alaska (Johnson 1982) and later in British Columbia (Watson and Smith 1996). However in Canada, no management solution has been found due to a range of factors including a lack of clarity around the rights of local First Nations who reserve the right to hunt sea otters for social and ceremonial purposes, regional differences in value, differences between stakeholder groups, and the legislative requirements of managing a listed species (DFO 2014). These governance questions and the diversity of values have created a lose-lose situation for management agencies because no single management strategy is likely to increase the value of the system for all stakeholders in all regions.

In our analysis, we examine how four services responded to different management scenarios both in aggregate, and decomposed into regional and local scales to explore how resolution and access influence the representation and realisation of benefits. We compare how the rank of the management alternatives is influenced by the addition of non-fungible benefits, and how model assumptions and integration influence the treatment and representation of uncertainty. Our goal is to test whether more spatially resolved services can identify benefits that make EBM more legitimate to stakeholders, and provide managers a broader set of indicators with which to develop more salient management alternatives.

### **Habitat suitability models**

Models of potential habitat suitability are increasingly common for marine species, and are now firmly rooted in correlative analyses (Robinson et al. 2011). Such models, including statistical (e.g., Generalised Additive Models) and machine learning methods (e.g., MaxEnt), combine species observations with maps of environmental predictors to quantify environmental (i.e., abiotic) suitability. In today's integrated management context, multiple habitat maps may be required to understand how a social ecological system responds to management. However, unevenness in available data (e.g., some service providers are surveyed intensively while others are managed without any detailed distributional or habitat information) can make the development of consistent habitat suitability models across a range of species problematic, if not impossible. In such cases, using a habitat suitability index provides an alternative.

Habitat suitability index models have a long pedigree clearly rooted in the need to support species management (USFWS 1981). Conceived in the 1980s by the United States Fish and Wildlife Service to support population impact assessments, the approach was born in a data-poor context where management decisions were nevertheless necessary. Instead of correlations, it relies on conceptual models developed by species experts (USFWS 1981, Van Horne and Wiens 1991, Wintle et al. 2005), allowing suitable habitat to be predicted without detailed distributional data. This presents an alternative to the relatively data intensive correlative approaches, and can perform as well as statistical models when evaluated against independent validation data (Chapter 3).

However, such maps of potential habitat, while useful for understanding the environmental limits of a species and widely used for policy analysis (e.g., Cheung et al. 2008), generally provide little insight into the species' ecological role, and are of limited use to tactical management. To overcome these limitations, habitat models must move beyond where a species may be (i.e., its potential habitat defined by abiotic constraints), to where it is actually likely to occur (i.e., its realised habitat) (GREGG et al. 2013). This translation of potential to realised represents the next frontier in habitat modelling (e.g., Chapter 3) and requires consideration of biologically favourable conditions, as well as barriers to movement (Soberón

and Nakamura 2009). Given the importance of realised habitat predictions for management, novel methods of translating predictions of potential habitat to realised habitat would improve the credibility of models supporting EBM. We present such an approach here.

## **Methods**

In this analysis, we predict the distribution of four ecosystem services derived from the biomass of 10 important nearshore species or functional groups: sea otters (*Enhydra lutris*), red sea urchins (*Mesocentrotus franciscanus*), geoduck clams (*Panopea generosa*), dungeness crab (*Metacarcinus magister*), small edible clams, reef fish (*Sebastes* spp.), lingcod (*Ophiodon elongatus*), and 3 kelp groups (the canopy kelps *Macrocystis integrifolia*, *Nereocystis luetkeana*, and other macroalgae). These ES providers are important ecologically, economically, and socially to various stakeholder groups along the coast (Klain and Chan 2012, Wieland et al. 2016; Chapter 4).

We predict realised biomass distributions under 4 management scenarios, and consider how services translate to benefits using 3 access levels. The data flow includes: defining potential habitat, translating this to realised habitat (using hypothesised species interactions) under different management scenarios, predicting the resulting biomass distribution, aggregating the biomass and services for each scenario at each access level, and translating the resulting services to spatially resolved benefits. Each of these steps is described in turn, below.

### **Habitat and biomass distributions**

We began by describing the potential habitat of ES providers using envelope models. Envelope models use a habitat suitability index (Van Horne and Wiens 1991; Chapter 2) to express how abiotic factors influence habitat suitability. For each species, we hypothesised its potential distribution from abiotic predictor variables using simple functional relationships. We combined the hypotheses arithmetically to define potential habitat on a scale of 0 to 1. We reviewed the potential habitat models with local experts to ensure they reflected the best available ecological understanding of how each species is distributed according to the available oceanographic variables (Table 5.1).

To extend these models of potential habitat suitability to realised habitat, we transformed abiotic habitat to realised suitability using three inter-specific ecological relationships (Fig. 5.2). Along with direct predation by sea otters, we included the cascading effect of increased kelp habitat from predator release, and the subsequent improvement of rockfish habitat through mediation – the effect one species on another via a third, intermediary species (Dill et al. 2003). All interactions were a function of the overlap of species distributions (see below).

To relate these ecological dynamics to management actions, we defined four management alternatives each resulting in a different realised habitat for sea otters (Fig. 5.2). The baseline scenario (M0) represents the otter-extirpated state under which coastal invertebrate fisheries were developed. The Laissez-Faire scenario (M1) leads to an equilibrium state where sea otters are at carrying capacity throughout the study area. The two intermediate scenarios create increasingly detailed spatial patterns of otter presence and otter absence: Regional management (M2) excludes sea otters from the central portion of the study area (i.e., Clayoquot and Nootka Sounds), and local management (M3) excludes sea otters to a distance of 5 km from 36 existing coastal communities (Fig. 5.1). The intermediate alternatives provide different scales of protection to a portion of the valued invertebrate biomass. Each management scenario results in a different realised otter habitat, which then drives changes in the realised distribution and abundance of their prey, kelp, and kelp-associated rockfish.

We assumed each management scenario led to an equilibrium state. This allowed us to use the ideal free distribution to represent the cascading changes in species abundance and distribution. Christensen et al. (2014) use the ideal free distribution to initialise the spatially-explicit population model Ecospace, and we adopt their approach here. For every cell ( $N$ ) in the model with a realised habitat suitability for species ( $spc$ ) greater than 0, we assigned a biomass proportional to the suitability in that cell ( $C_{N,spc}$ ):

$$B_{N,spc} = \frac{C_{N,spc}}{TC_{spc}} * B_{spc} \quad \text{Equation 1}$$

Where  $TC_{spc} = \sum_N C_{N,spc}$  is the sum of all habitat suitability values for species  $spc$ , and  $B_{spc}$  is the total biomass of the species in the study area.

Both  $B$  and  $C$  are a function of the management scenario. Thus, to effectively apply the ideal free distribution we needed scenario-specific estimates of biomass and predictions of realised habitat.

We estimated biomass for each ES provider for each management scenario by assuming it scaled linearly according to habitat suitability between the baseline and carrying-capacity states. The biomass values for these two states were taken from Chapter 4 (Table 5.2), under which each species ( $spc$ ) had either a maximum ( $B_{max_{spc}}$ ) or a minimum ( $B_{min_{spc}}$ ) biomass. For the intermediate scenarios ( $S$ ), the biomass for each species ( $B_{spc,S}$ ) was estimated by linearly scaling the proportion of maximum biomass according to the corresponding change in realised habitat suitability ( $HS_{max_{spc}} - HS_{min_{spc}}$ ) for the species:

$$B_{spc,S} = \frac{B_{max_{spc}} - B_{min_{spc}}}{HS_{max_{spc}} - HS_{min_{spc}}} * HS_{spc,S} + B_{min_{spc}} \quad \text{Equation 2}$$

Where  $HS_{spc,S}$  is the realised habitat suitability for an intermediate scenario. This effectively scales the biomass linearly between these two extreme states based on the realised habitat suitability for the scenario (Fig. 5.3). This process ensured that biomass was scaled not only for each management scenario, but also consistently across the scenarios, avoiding potential (incorrect) variability in the resulting carrying capacity.

We parameterised the transformation of potential to realised habitat suitability for sea otter prey using hypothesised vulnerability to predation (Fig. 5.4). High value, highly accessible sea otter prey (urchins and crabs) were assumed to have high vulnerability, while geoducks and small clams were assumed to have moderate vulnerability. For geoducks the lower vulnerability was based on reduced accessibility, while for small clams it was based on the lower nutritional value of this group. For kelp groups, realised habitat was assumed to be highly vulnerable to sea urchin predation because a small number of urchins can have a disproportionate effect on kelp abundance (urchins eat kelp holdfasts, thus preventing kelps from occurring even without eating much kelp tissue). Finally, given that kelp forests add considerable habitat complexity to rocky reefs, and that habitat complexity is correlated with improved rockfish recruitment (Johnson 2007), we allowed the realised abundance of kelp to exert a mitigating effect on reef

fish habitat suitability by increasing the suitability where kelp co-occurred by as much as one third (Fig 5.4). With no data with which to estimate the change in reef fish abundance, we used one third because habitat mediation is one of three possible mechanisms for kelp to increase rockfish production (Markel 2006).

To maximise consistency across management scenarios, the vulnerability curves were parameterised so that reductions in habitat suitability (from potential to realised) reflected the observed change in biomass.

Any representation of predator-prey dynamics must consider the role of foraging patch size on the trophic interactions. For sea otters, we followed Gregr et al. (2008) and used a circular moving average window with a radius of 3 km to define a foraging patch. This smoothed the sea otter habitat map producing more consistent areas of influence on the prey distributions. The other species in this analysis have much higher site fidelity because of their low mobility (particularly the infaunal invertebrates). We therefore assumed it was sufficient to treat each 100 m x 100 m (1 ha) cell as a potential habitat patch. We argue this is a reasonable approach if cells are large compared to the animal's foraging range.

Finally, since the ideal free distribution allocates biomass to any area with suitability greater than 0, this poses the ecological question of whether there is a suitability threshold below which a habitat is unlikely to be occupied. Here we followed Akçakaya et al. (1995) and used a threshold to avoid small, isolated patches of biomass which may not be ecologically reasonable. Without data specific to this point, we applied a minimum suitability threshold of 0.20 to all species. This allows species to establish themselves in even the smallest patches if the habitat suitability is moderate or high.

### **Estimating benefits**

The resulting distributions of ES provider biomass can be characterised as ecosystem supply (sensu Tallis et al. 2010). To compare management scenarios, we estimated the dollar value of four ecosystem services arising from this supply: 1) the landed value of established nearshore fisheries; 2) the supplemented catch of valued finfish arising from increased primary production (modelled as high trophic level coastal species external to our nearshore model); 3) the

contribution of sea otters to wildlife-based tourism; and 4) carbon sequestration. All values were expressed in 2015 Canadian dollars, with no discounting.

To illustrate the relationship between ecosystem service supply, benefits, and management scenarios, we consider the distribution of ecosystem services at three levels of access. *Global* accessibility assumes beneficiaries can access all resources in the study area regardless of their distribution. This is the most commonly used assumption and it implies that any change in service supply translates directly to realised benefits. To examine the validity of this assumption, we consider two increasingly resolved levels of access: *regional* accessibility assumes only beneficiaries within a sound can access its services (Fig. 5.1); and *local* accessibility assumes access extends to 5 km of coastal communities. The 5 km limit represents a reasonable resource harvesting day trip in a small, open boat. We examine the distribution of service supply at these three resolutions, and how access influenced the benefits derived. Finally, we compare how the benefits differ by management scenarios across the regional and local access levels.

The distribution of ES supply, based on estimates of biomass (Chapter 4) and the relative habitat suitability maps developed here, are presented as point estimates (i.e., only a single realised distribution map is produced for each species). We introduced uncertainty by randomly sampling key parameters in the service valuation functions, emphasising the uncertainty around the many assumptions needed to translate service supply to monetary value. Because the randomisation results were not normally distributed, we used violin plots, with medians and percentiles, to display the results. This allowed the differences in benefits at different access levels, under different scenarios, to be compared while providing intuitive visualisation of the uncertainties.

While acknowledging the many uncertainties in the estimates of biomass and habitat suitability, we focused on the uncertainty of monetising metrics of supply because this uncertainty is much higher than the parametric uncertainty around the derivation of the biomass estimates (Chapter 4). Estimating the uncertainty in the habitat suitability predictions

is an important task that would be particularly relevant when comparing small areas within the study area. However, this data-intensive task is beyond the scope of this Chapter.

### ***Landed value***

For each established commercial invertebrate and rockfish fishery (urchins, geoduck clams, Dungeness crab, other clams, and lingcod) we estimated the dollar value of the annual catch ( $V_C$ ) by combining the predicted biomass with 10 years of landed value data and a constant fishing mortality (Table 5.3). For each access level and management scenario, we took the point estimate of accessible biomass for each species ( $spc$ ) and estimated a value distribution using:

$$V_{C,spc} = B_{spc} * M_{spc} * V_{spc} \quad \text{Equation 3}$$

Where biomass (in tonnes, t) is the sum of biomass within the access area as predicted by the idea free distribution,  $M$  is the fishing mortality rate, and  $V$  (M\$/kt) is the 10-year average of the landed value. The biomass was scaled ( $10^{-3}$  kt/t) to convert t to kt giving  $V_C$  in M\$/year for each species, access level, and management scenario.

The value distribution was generated by randomising  $V_{spc}$  using a truncated normal distribution (Trautmann et al. 2014) applied to the species-specific mean and standard deviation of the annual landed value data. Truncated normal distributions were used throughout the benefits model where values less than 0 were unreasonable.

### ***Services from increased primary production***

Primary production from kelp in an otter-dominated system is significant, rivalling that of phytoplankton in coastal systems (Chapter 4). We model two services from this increased supply of organic carbon. First, we consider the nutritional supplement to coastal ecosystems from the particulate organic matter produced (e.g., Koenigs et al. 2015). Second, following Wilmers et al. (2012) we estimate the value of carbon sequestration from the portion of the surplus production exported to the deep ocean.

We defined annual surplus (i.e., net) primary production ( $NPP$ ) from kelp as the production not consumed in the ecosystem models described in Chapter 4. We calculated this net production individually for each of the 3 kelp groups (Macro, Nereo, and Other) according to:

$$NPP_{kelp} = \sum_{spc} \left( B_{spc} * \frac{P}{B_{spc}} * (1 - EE_{spc}) \right) \quad \text{Equation 4}$$

Where  $B_{spc}$  ( $\text{g m}^{-2} \text{ year}^{-1}$ ) is the steady state biomass for each kelp group (*spc*),  $P/B$  is the annual production/biomass ratio, and  $EE$  is the ecotrophic efficiency (i.e., how much biomass was accounted for in the model). To represent uncertainty in density dependent effects on  $P/B$  and  $EE$ , these parameter values were sampled from triangular distributions declining from their maximum to their predicted (by the Ecosim model) minimum.

The  $NPP$  in Equation 4 represents kelp detritus from senescence or storm action and has 3 possible fates: retention in the marine food web, loss to the deep ocean, or loss to intertidal or terrestrial ecosystems. Data on such partitioning is unavailable, although studies in California have estimated giant kelp wrack (stranded on shore) deposition to be over  $500 \text{ kg m}^{-2} \text{ year}^{-1}$  (Dugan et al. 2011). Each of these partitions provides important services. For example, wrack is understood to support coastal and land ecosystems through the enrichment of amphipods (Polis and Hurd 1996) and probably mussels and other species. The primary production that remains in the coastal food web contributes to the production of higher trophic levels, evaluated here as a nutritional supplement, while the loss of kelp detritus to the deep ocean contributes to carbon sequestration (Wilmers et al. 2012).

We modelled this partitioning by first estimating the  $NPP$  lost to wrack ( $NPP_W$ ):

$$NPP_W = L_W * NPP \quad \text{Equation 5}$$

Introducing uncertainty by sampling  $L_W$  from a triangular distribution with parameters (min = 0.01, mode = 0.10, max = 0.2) based largely on intuition.

From what remains, we represented the flux to deep ocean ( $NPP_D$ ) as:

$$NPP_D = L_D * (NPP - NPP_W) \quad \text{Equation 6}$$

with uncertainty again introduced by sampling  $L_D$  from a triangular distribution with parameters (0.01, 0.25, 0.5) adapted from the deep flux scenarios explored by Wilmers et al. (2012).

If  $NPP$  is not lost to the landscape or the deep ocean, we assumed it was retained in the marine food web:

$$NPP_S = NPP - NPP_W - NPP_D \quad \text{Equation 7}$$

This portion of the  $NPP$  ( $NPP_S$ ) provides a nutritional supplement to many marine species, including valued commercial finfish.

### ***Nutritional supplement***

We valued the nutritional supplement ( $V_{NS}$ ) by estimating its potential for increasing the abundance of large commercial finfish. We used published trophic transfer efficiencies to move the particulate organic biomass up 3 trophic levels to the most valued finfish, and averaged their landed value to estimate the dollar value of the increased production:

$$V_{NS} = NPP_S * TTE_1 * TTE_2 * TTE_3 * LV \quad \text{Equation 8}$$

The dollar value of  $V_{NS}$  was estimated from  $NPP_S$ , three trophic transfers, and an estimated landed value ( $LV$ ). The first ( $TTE_1$ ) represents the transfer from primary production to primary consumers and has an estimated mean = 0.25 (Wade 2000 cited in Perry and Schweigert 2008). The subsequent transfers ( $TTE_2$ ,  $TTE_3$ ) are between predators and prey and use a mean = 0.1013 and standard deviation = 0.581 (Pauly and Christensen 1995). We introduced uncertainty at each trophic transfer by randomly sampling from a truncated normal distribution using the above parameters.

Our estimate of the dollar value of this supplemented catch also included uncertainty. We randomly sampled  $LV$  from a triangular distribution bounded by the average annual landed value (2001 to 2010, adjusted to 2015 prices) of the least and most expensive commercial finfish (i.e., rockfish at 1.74 \$/kg and halibut at 8.53 \$/kg) (Province of British Columbia 2014), with a mode of 2.77 \$/kg – the weighted average of the adjusted annual landed value of all commercial finfish (i.e., halibut, lingcod, rockfish, and salmon) across the 10 years.

### ***Carbon sequestration***

We estimated the amount of carbon sequestered using estimates of deep ocean flux, % dry, and % carbon from Wilmers et al. (2012). We predicted the dollar value using the long-term average California market price (CPI 2016) as a proxy for the social cost.

We estimated the value ( $V_C$ ) of carbon sequestered in the deep ocean ( $NPP_D$ ) by first converting  $NPP_D$  to dry carbon, and multiplying by the annual dollar value:

$$V_C = NPP_D * \%D * \%C * V_{tonne\ C} \quad \text{Equation 9}$$

The  $NPP_D$  was dried using % Dry (%D, mean = 0.173, SD = 0.019) and converted to % Carbon (%C, mean = 0.266, SD = 0.028) with values estimated by Wilmers et al. (2012) for giant kelp (it was assumed that %D = 1 - % wet, the reported value). Uncertainties were included with both these estimates by sampling from a normal distribution. The value of a tonne of carbon ( $V_{tonne\ C}$ ) (mean = \$15.26/tCO<sub>2</sub>, SD = \$2.8/tCO<sub>2</sub>) was based on the average annual price of carbon (adjusted to 2015 Canadian dollars) from the California Carbon Exchange since inception (CPI 2016), sampled from a truncated normal distribution. A conversion factor for C equivalents to CO<sub>2</sub> based on the molecular mass ratio (CO<sub>2</sub>/C = 44/12) was also needed.

### ***Tourism***

Our estimated value of sea otters to wildlife tourism is based on the willingness to pay (WTP) for an increased likelihood of sea otter encounters and the predicted increase in sea otter abundance. However, unlike the other three services considered, the tourism service also needs to consider the availability of tourism infrastructure. Thus, for a particular scenario (i.e., sea otter abundance) the value of tourism ( $V_T$ ) is specific to particular access areas ( $a$ ), and was estimated as:

$$V_{T,a} = V_{visit} * B_{prop} * N_{V,a} * N_{prop} \quad \text{Equation 10}$$

Where  $V_{visit}$ , a random sample of amount spent per visitor, was drawn from a normal distribution (mean = \$227,75, standard deviation = \$53.37) based on WTP data collected by Martone et al. (see Chapter 4). We assumed this WTP value applies to the Laissez-Faire scenario

where sea otters reached carrying capacity, and scaled it for other scenarios linearly according to sea otter abundance ( $B_{prop}$ ).

$N_{V,a}$  is the number of visitors to the west coast of Vancouver Island drawn from a normal distribution with the mean (776,310) and standard deviation (22,170) from 10 years of visitor statistics to Pacific Rim National Park, an internationally renowned park that attracts visitors to both Barkley and Clayoquot Sounds (Parks Canada 2014). These data were scaled for regional access areas ( $a$ ) using visitor intent data from Martone et al. as a proxy for tourism infrastructure.  $N_{prop}$  is the proportion of visitors who declared an intention to go on a wildlife tour (27.6%, Martone et al. in prep) and was used as a constant.

## **Results**

With 10 ES providers, 4 management scenarios, and 3 access levels, our analysis foreshadows the complexity inherent in EBM. Rather than displaying the myriad possible results, we focus on illustrating how the distribution of benefits can influence their perceived value to different stakeholders.

We first present the results of the habitat suitability models, and the translation of potential habitat maps to realised habitat. We then examine how service production changes in response to the management alternatives, and finally illustrate how measuring the distribution of ES supply can uncover a wider set of benefits, some of which can lead to a difference in the rankings of the alternatives.

### **Habitat suitability**

The habitat suitability models (Fig. 5.5 - graphical equations) generated plausible maps of potential habitat for all species (Fig. 5.5 - suitability maps). Artefacts are evident in some of the habitat models, such as high pixel-to-pixel variability (rockfish habitat) and large blocks of habitat (e.g., Dungeness crab).

These artefacts are typically limitations of the predictor data. For example, the discrete nature of the Dungeness habitat prediction is driven entirely by the categorical predictor Bottom Type. The apparent patchiness is reduced for species with numerous, effective, continuous predictors

(e.g., red sea urchins; geoduck clams). However, for species with fewer (e.g., small clams) or less effective predictors (e.g., the salinity and temperature variables for Dungeness crab), the resulting patchiness is more pronounced. In the case of crabs, salinity and bottom temperature have no effect as the entire study area falls in the optimum range.

The high pixel-to-pixel variability is a function of the high resolution with which the rocky reef predictor was calculated. This variability is removed when the model is smoothed, as it was for sea otters which, with their greater foraging range, assumes they integrate their habitat suitability over a larger area.

### **Potential to realised habitat**

Translating potential to realised habitat and scaling the amount of biomass to distribute was done independently for each species interaction, for each alternative. The biomass and the realised habitat must scale consistently to ensure that the cells with the maximum suitability have the same biomass across all management scenarios (i.e., that carrying capacity is constant). While this was achieved for some species, it could not be achieved for others (Table 5.2). For Dungeness crab, realised habitat suitability could not be reduced to match the change in biomass because of insufficient overlap with sea otter habitat. For the Macro and Other kelp groups, the reduction in realised sea urchin habitat was not enough to sufficiently increase the realised kelp habitat suitability. Similarly, for the rockfish and lingcod groups the realised kelp habitat could not sufficiently improve the habitat distribution to allow the change in habitat suitability to approach the predicted increase in biomass.

A mismatch between the predicted change in biomass and the associated change in habitat suitability leads to different carrying capacities in the model cells under different management alternatives. This variability is of little consequence to our analysis because our benefits are aggregated over relatively large access areas. It would, however, reduce confidence when comparing small patches.

### **Service production and distribution**

The distribution of benefits is first and foremost a function of the service providers. Many direct services (e.g., provisioning, sports fishing, subsistence) can thus be visualised from the realised

habitat suitability maps. Examining the distribution of service provision at three resolutions (Fig. 5.5 - Bar graphs) gives insight into this relative productivity of the different regions, and how it changes across scenarios. For example, regionally, geoduck clam and red sea urchin habitat is concentrated in Clayoquot and Nootka respectively, while kelp is predicted to be most abundant in Barkley and Kyuquot. At the local scale, small clams and geoducks have the highest proportions near coastal communities, suggesting higher local availability.

Allowing sea otters to reach carrying capacity (Laissez-faire scenario, M1) results in sea otter biomass distributed about uniformly across the 4 regions in the study area, with a large proportion away from local communities. The other management scenarios reflect the management strategy applied, with sea otters absent from Nootka and Clayoquot in the Regional scenario (M2), and from Close to communities in the Local (M3) scenario.

The Laissez-Faire scenario more than quadruples the total kelp supply compared to baseline (i.e., the otter-absent scenario), with Barkley Sound showing the greatest increase and Clayoquot the least. Approximately 1/3 of this biomass is produced close to communities. While there is little difference in the total biomass between scenarios M2 and M3, significant differences in distribution are evident at both the regional and local level. Laissez-Faire also almost doubled the total biomass of rockfish, with the greatest increase predicted for Barkley and the lowest for Clayoquot. There was little difference in the predicted rockfish distribution and biomass between M2 and M3.

Unsurprisingly, red sea urchins and Dungeness crab showed the greatest response to the changes in realised sea otter distribution, with M1 predicting the virtual extirpation of these species within the study area (to 50 m depth, the limit of sea otter foraging).

These losses were mitigated, though differently, by the Regional and Local alternatives. Regionally, under M2, sea urchins were at 60% of baseline and evenly distributed between Nootka and Clayoquot; in M3 they were less than 25% of baseline, but distributed evenly across regions. For Dungeness crab, M2 retained over 75% of baseline compared to less than 25% for M3; in both cases biomass was concentrated in Clayoquot. The Local scenario reduced biomass

for crab by over 75% and for urchins by over 80%, with virtually all the retained biomass close to communities.

Under M1, geoduck and small clams show approximately 20% loss from baseline biomass with a largely static proportion across access levels. M2 and M3 both show a slight reduction in biomass loss over M1, with Nootka and Local showing notable differences between these two scenarios.

### **Benefits from the different scenarios**

Assuming all services are equally valued, our analysis suggests the Laissez faire scenario (M1) leads to the highest change in value relative to the no sea otter baseline (M0). Regional management (M2) was predicted to result in the lowest value, with Local management (M3) in between (Fig. 5.6). We estimated all services as a change from the M0 baseline rather than in absolute terms because the transition from this baseline is already underway, and it represents the value anchor for many stakeholders.

When decomposed, results are similar to Chapter 4, with the aggregate score dominated by tourism, whose median contribution of 50.6 M\$/year under M1 comprised over 80% of the predicted value (Fig. 5.7). The median value of the supplemented catch was 8.88 M\$/year, while for carbon sequestration it was 0.82 M\$/year. This comes at the expense of a median catch loss of 6.42 M\$/year. M1 ranked highest on tourism and supplemented catch, while M2 was best for minimising Catch losses. M3 had intermediate values across all services.

For stakeholders whose primary value is the cost to invertebrate fisheries, M2 would be preferred, while for those valuing the supplemented catch of finfish, there is little apparent difference between M2 and M3 (Fig. 5.7). However, when services are examined at higher spatial resolution, the distribution and accessibility of benefits can be clarified, and additional benefits, such as equity and naturalness, defined.

For example, resolving the catch loss benefit at the regional extents allows its distribution to be considered regionally, a potential indicator of equity. In this case, M3 may be considered more equitable than M2 because the loss is shared proportionally by all regions (Fig. 5.8). Exploring

benefits regionally thus supports the conversation about whether shared (and proportional) loss (i.e., M1 or M3) is preferred to regionalised costs and benefits (i.e., M2).

When examined locally (Fig. 5.9), the losses close to communities are mitigated best by M3, while distant losses, at 3 times local losses, are minimised by M2. As well as being another indicator of equity, reduced catch loss close to communities is also a clear indicator of subsistence. The question of equity here turns on what is just in terms of resource access. If there nourishing coastal communities has value, then M3 may have higher value than M2.

Regional extents also allow us to use ecological considerations such as naturalness to examine whether the supplemented catch under M2 and M3 are really of equal value. Under M3, this benefit is distributed across regions in pattern more similar to M1 (Fig. 5.10). If M1 is assumed to be the most natural state (by virtue of being Laissez-faire), then M3 preserves more of this naturalness than M2 and may thus be preferred, all other things being equal.

## ***Discussion***

### **Trade-offs**

Evaluating trade-offs depends on the benefits and costs realised by the relevant stakeholder groups. It is understood that these can vary, but for EBM to be seen as legitimate, stakeholders must see their values reflected in the ES benefits represented. While we did not address the question of stakeholder value here, our valuation of services and their translation to benefits nevertheless provides insights into the trade-offs that can be anticipated in this system.

In our study area, we predict that a system with sea otters will produce more aggregate dollar value than a system without otters. However, when the services are considered individually, the management alternatives generate interesting (and different) compromise solutions, but no win-wins. This is inevitable as sea otters compete directly with the invertebrate fisheries. However, our Regional management example, which excluded otters from some of the most productive invertebrate areas, suggests the dollar value could be maximised by structuring spatial management to correspond to regional productivity. This is especially true for cases such

as ours, where the habitat of some valued invertebrates (clams and crab) is distinct from high quality kelp habitat.

The asynchronous response of benefits estimated at different access levels to the different management alternatives (e.g., compare Total and Close catch loss in Fig. 5.9) invalidates the often made assumption that supply translates directly to benefit. And these examples only scratch the surface of the myriad indicators of benefit that can be derived with increased model resolution. We expect such indicators will emerge however model resolution is deliberately improved, not just geographic space. For example, the richness of the catch loss could be expanded to include the component species, or the seasonal aspect of sea otter distribution could be used to inform the tourism benefit.

### **Justice, legitimacy, and salience**

Limiting trade-off analyses to fungible indicators lacks legitimacy because highly valued social and environmental benefits are not represented. Our analysis shows how improving the spatial resolution of service valuation uncovers indicators relating to ecological integrity and equity. Such indicators would seem impossible to develop in an aspatial context. These indicators can inform questions of equity that arise when those who benefit most from different, often conflicting, services are different stakeholder groups. For example, commercial fishermen and First Nations often prefer fishing or subsistence benefits over tourism, despite the potentially higher value of that service. This is rooted in cultural and traditional values, where those with strong ties to coastal living often prefer harvesting their own seafood over providing tourism services.

Geographic factors can also influence perceptions of equity. For example, residents of coastal communities may value local fisheries and local processing much more than fisheries that extract the resource for processing elsewhere. This can be characterised as a trade-off between situational vs. extractive benefits, and the ratio of the two could bundle a variety of values related to justice and equity.

How benefits from different management actions flow to different groups can also be an important aspect of equity. In our study area, the invertebrate fishery is concentrated in the

hands of a few fishers, often living some distance from the resource. Thus, the question of who benefits may often be the fundamental issue regarding equitable management, and the social acceptance of alternatives.

Thus, by allowing trade-offs between local, regional, and global communities to be more justly assessed, indicators of accessible benefits are crucial for representing fundamental equity problems. We note that this is in addition to, but distinct from, the value of well resolved benefits to detecting marginal changes in services (Chan and Daily 2008, Grêt-Regamey et al. 2014).

Access is a key component of such equity indicators, and our admittedly simplistic grouping of benefits nonetheless emphasises the connection between benefits and place. Our definitions of regional equity and local subsistence support the idea that many benefits are best perceived at particular resolutions. This scaling of benefits to the relevant stakeholder values represents an important step to ensuring the legitimacy of EBM.

Broadening the suite of potential benefits also allows managers to develop more legitimate alternatives, like local exclusion, that may be reflective of management practices prior to the extirpation of sea otters (Szpak et al. 2012). The granularity provided by well-resolved benefits also provides managers the tools to include potentially more salient measures to accommodate regional differences in value, while still meeting ecological concerns, possibly at a variety of resolutions.

The value of scaling benefits to stakeholders and increasing the suite of alternatives available to managers was recognised in the decision support literature some time ago (McDaniels et al. 2006). That this has yet to reach the ecosystem modelling and ES mapping communities illustrates the very real inter-disciplinary challenges of making ecosystem models useful to decision makers.

### **Bounding model complexity**

Mapping the distribution of resources is now fundamental to studies of ES across marine and terrestrial systems, ranging from local to global scales. This requires estimates of species

abundance, usually from population models, and habitat suitability models to map the distributions. The predicted distributions of ES providers is then translated to stakeholder benefits using a variety of benefit functions. Each of these activities is represented by largely discrete group of researchers, working with their own abstractions of the real world, defined across the axes of richness (ES benefits), time (population models) and space (habitat models) (Geger and Chan 2015).

Along each of these axes, researchers are doubtless working at the limit of their knowledge and technical capacity. It therefore stands to reason that the integration of the most complex components would be beyond both our understanding and technical means. Further, the integration path from data collection to scenario evaluation is long, and replete with uncertainties. Understanding these uncertainties is critical for integrated model development as they can be used to develop reasonable limits on the precision desired from sub-models.

We argue that rather than striving for increasingly complex models (e.g., Parrott 2011, Purves et al. 2013), integrated benefit models would progress faster with a focus on adapting and integrating what we know, including our uncertainties, using the decision context to drive the necessary complexity. Such models would integrate the necessary components in a way that minimises complexity when the realised precision or detail is not required given the larger uncertainties elsewhere in the model. Such data-informed, hypothesis-driven, holistic models of social-economic systems will make ecosystem models more useful to quantitative policy analysis (Morgan and Henrion 1992). They are also likely to make the overall system more intelligible for everyone - ecologists, stakeholders, and managers - than complex, data-driven analyses of the parts.

Integration of ES benefits and ecosystem models is especially relevant to bounding model complexity. As described in the previous section, broadening the basket of benefits is essential to making more legitimate and salient management decisions. Our integrated analysis show how increasing the bounds of benefits considered can actually reduce the necessary model complexity. This is because the uncertainty in estimating benefits can help identify a threshold

beyond which increased ecological precision will have no further influence on the precision of the integrated model.

### **Habitat predictions**

Process-based models (e.g., the habitat suitability index) can generate approximations of potential habitat that are deemed reasonable by local species experts, given the environmental data available. In certain contexts they can be as good or better than statistical models (Chapter 2). Process models have 2 additional advantages over correlative ones. First, they are easier to explain and interpret because they begin with understanding. Second, they can preserve valuable observational data for model validation, rather than using it to develop correlations. For well-understood species (i.e., those for which processes can be readily described) the observational data can serve as a valuable test bed to compare different species-habitat hypotheses. Process models are also useful in the many situations with limited distributional data (e.g., for rare species, or in jurisdictions with limited resources). This rapid prototyping ability makes such habitat models a valuable and potentially sufficient (depending on objectives) tool for exploring marine resource management questions.

Management (vs. policy) questions will often require predictions of realised, rather than potential habitat. This is especially true (as in our case) when management alternatives influence the distribution of individual species. Distinguishing potential from realised habitat is a challenge because the diversity of species interactions, across a range of life histories, remain largely impossible to parameterise. In our analysis we used the strength of trophic interactions, species abundance, and habitat overlap to model the change from potential to realised habitat with some success. Without these biological constraints, the predicted benefit distributions would have lower confidence. Such indirect, inferential methods may have broad application in the translation of ecology into credible model components (i.e., in model design).

Using changes in biomass to inform potential to realised habitat translation provides a unique opportunity to compare the two models. Analytically, how well the change in habitat suitability can reproduce the change in biomass predicted by the population model can be interpreted as an indicator of habitat model quality. Low agreement implies insufficient overlap between the

habitats of the predator and prey species. For example, the reduced, realised sea urchin habitat did not allow a corresponding increase in realised kelp habitat suitability anywhere near what would be expected from the biomass numbers (Table 5.2). This implies lower confidence in one or both of the potential suitability models. We suggest such a 'model correspondence distance' can serve as an indicator of agreement at the interface of model components.

### **Assumptions and uncertainties**

In this analysis we integrated data across scales, into models of population dynamics, habitat suitability, and ecosystem service benefits for an interacting group of valued species in a coastal ecosystem. This model scope requires good resolution on both the space and richness axes. Spatial resolution is needed to ensure realised habitat can be effectively estimated and barriers to access realistically represented. Richness is necessary to represent the many valued ES providers of the coastal ecosystem, their habitats and interactions, and the benefits that arise.

Model integration requires designing how model components will fit together. We believe understanding the uncertainties in the components can inform this design. When developing our model we found the necessary integration assumptions often had more uncertainty than the individual model components, especially in the benefits model and at the sub-model boundaries. For example, the uncertainty (represented as random distributions) in the social and economic valuation of ES production swamped the parametric uncertainty in the Ecopath model (Chapter 4) and was relatively insensitive to structural uncertainty in the habitat models.

While bad for model precision, these various uncertainties can be used to improve model generality by relaxing the precision required from high-precision sub-models. It also, by forcing the necessary assumptions to be articulated, allows our confidence in them to be expressed and integrated into estimates of overall model confidence. Articulating the uncertainty in the assumptions underlying the benefits model thus informed the confidence we should place in the larger model, an uncertainty that can be intelligibly represented by violin plots.

While we considered only a handful in this illustrative example, there is no real limit to the number of assumptions that can be included in this way, although care would be needed to ensure the uncertainties are independent (i.e., not being double-counted). If the assumptions

considered are also assumed to be the most uncertain, and are structured conservatively, then the resulting models, while perhaps not entirely 'true', may at least provide a reasonable reflection of our understanding.

We structured our supplemented catch benefit to be conservative by valuing it with only commercial landed values. In fact, the recreational sector is estimated to generate approximately 10 times the value of the commercial fishery (Okey and Wright 2004), and in BC it is allocated 12% of halibut harvest and 5% of the total harvest for each of sockeye, pink and chum, with priority to sports fisheries on chinook and coho salmon (Gislason 2006). While the situation is rather complex, assuming a 10% allocation of the valued finfish biomass to the sports fishery seems reasonable. Combined with its higher value, this would lead to a 1.9-fold increase in our predicted supplemented catch value. Additionally, we only considered the supplement from NPP. Had we included the potential supplement from primary and secondary consumers (e.g., zooplankton, herring) the resulting finfish biomass would be considerably higher.

On the other hand, we assumed surplus primary production was entirely consumed by valued finfish at higher trophic levels and that these are largely exploited (Pauly et al. 1998). While some diversions from the flow of kelp detritus to valued finfish can be imagined, parameterising these diversions would be challenging. Given that the uncertainty around the predictions is already high, we chose to assume these diversions were within the represented uncertainty.

The omission of other benefits obtained from kelp makes our valuation of increased primary production even more conservative. These include the local value of kelp forests for nearshore navigation; the cultural value of rockfish to local communities; and the value of wrack to coastal terrestrial ecosystems. We expect the inclusion of these and other benefits would notably increase the value of surplus production, particularly to local stakeholders.

With respect to the tourism benefit, we made no allowance for how it may be affected by the type of sea otter management applied. Currently habituated to a non-interfering human

presence, these skittish animals are likely to respond to any management action in a way that reduces the tourism benefit, but how much is difficult to know.

This is an example of known unknowns, something such ecosystem models are full of. Others include social factors like changing demand for (and hence the price of) seafood, and ecological ones such as the likelihood of sea otter populations being decimated by disease. The considerable uncertainties in social-ecological systems support our assertion that EBM is not constrained by low model complexity or technical skill, but by social-ecological knowledge and our ability and willingness to confront such uncertainties. In the short term, the best we can do is treat known unknowns explicitly by identifying and integrating those we think the most egregious. In the longer term, studies focused on particular social or ecological questions, using purpose-collected data, may fill some knowledge gaps. However, as in nature, uncertainties and surprises will be ever-present.

### ***Limitations and future directions***

A clear next step is the integration of this model with a local decision model to see how well it can support real-world decision-making. The resulting, fully integrated EBM decision model, if not used directly for tactical management decisions, would at least contribute to an informed discussion of management alternatives.

The need for multiple habitat suitability models led us to choose the generality of process-based habitat suitability models over the precision of correlative ones. Revisiting the habitat models may improve model precision, and validating them with the model correspondence distance would represent an important innovation for evaluating integrated models. The habitat suitability index lends itself to an iterative, adaptive process where, starting with explicit hypotheses about species distributions, the index can be repeatedly updated and validated with additional data. Using a more structured approach such as multi-criteria evaluation (e.g., Store and Kangas 2001) may allow for more formal integration of the various predictors. Bayesian methods may also be useful for constructing credibility intervals.

In terms of model richness, the services we defined were intended to be illustrative rather than definitive. Considerably more data (e.g., infrastructure, demographics) could be brought to bear to both refine the benefits we used, and to uncover new ones. For example, identifying indicators of relational values (Chan et al. 2016) represents a potentially fruitful avenue to increased equity. However, as with uncertainties, dependencies among the benefits need to be considered to avoid double-counting them in quantitative assessments.

Our management alternatives were constructed for illustration rather than salience. Development of salient alternatives would leverage existing work in the region (Espinosa-Romero et al. 2011a) and elicit stakeholder views on strategies. This would be valuable since actually implementing spatial management of sea otters may be the most significant barrier to EBM in this system. Requiring active control, either through spatially-selective culling or re-location, it will be unpopular with some stakeholders. However, a spatially-explicit strategy is expected to have the advantage that some behavioural conditioning may be achieved, eventually reducing the need for lethal control.

A relevant alternative we could not implement but may reflect the current status quo is the random killing of sea otters. To those who see sea otters as destructive pests (Carswell et al. 2014), a strategy that simply keeps the population at some level below carrying capacity across the study area may be of interest. Unfortunately, our model does not support the temporal resolution needed to represent what would be a very dynamic ecosystem.

Indeed, it was the complexity of the temporal dynamics that led us to limit our model to the two equilibrium states, defined by the otter-present and otter-absent ecosystems. While dynamic approaches would likely be preferred in some cases, we argue that although the technical ability to develop such simulations exists, the knowledge to structure and parameterise them in a credible manner is largely lacking. We simply don't know enough about movement, dynamic growth rates, and changing trophic interactions to parameterise such models with much confidence. The pursuit of such knowledge would be fruitful, and is fully within the purview of ecosystem models.

## ***Conclusions***

Our analysis illustrates how the distribution of ES providers informs trade-offs not apparent when space is ignored. Spatially resolved indicators are central to ensuring EBM is seen as legitimate. Improved resolution also provides managers with the opportunity to develop more salient management alternatives. By measuring access to benefits, we uncovered indicators of ecological and social benefits rarely considered. At the regional scale we defined indicators of equity and naturalness that trade-off against economic value. At the local scale, we found subsistence could be characterised based on the proportion of catch loss near coastal communities. Such indicators are needed to increase the legitimacy of EBM to stakeholders, improve equity, and increase salience for managers.

Methodologically, our explicit consideration of key assumptions allows the associated uncertainty to be used to level the complexity of model components, and provide an estimate of overall model credibility. Our comparison of population and habitat suitability models represents a potential advance in the integration of inter-disciplinary models, an activity we expect would interest everyone engaged in mapping ecosystem services.

We have argued that EBM is not limited by a lack of complexity or technical skill, but by fundamental gaps in our understanding of social-ecological system function (Grega and Chan 2011). This resonates with calls for less model complexity (e.g., Merow et al. 2013), which we would couple with one for a more holistic view of ecosystem models, especially around the articulation and representation of significant assumptions. By integrating population, habitat suitability, and benefits models, driving them with different spatial management alternatives, and incorporating uncertainty in both model design and results, many of the challenges facing ES mapping and EBM can be overcome.

*Table 5.1: Environmental variables used to develop habitat suitability models.*

<b>Variable</b>	<b>Range</b>	<b>Description</b>
Depth	[HWL - 50]	In m, taken from a 20 m bathymetric model that includes depths from the high water line to 50 m (0 represents the low water line).
Rocky reef	[0, 1]	A rocky reef index based on Haggarty's (2015) application of the Benthic Terrain modeller to BC shelf waters.
Bottom type	(1,2,3)	Classes of bottom type (Hard, Mixed, Soft).
Exposure index (Total)	[0, 36]	In 100s of km. Total potential exposure based on fetch. Maximum value is 50 km * 72 fetch lines.
Exposure index (SE)	[0, 5]	In 100s of km. Total southeast exposure based on fetch. Maximum value is 50 km * 10 fetch lines.
Surface temp.	[11.5, 17.5]	In Celsius. Average surface temperature in summer obtained from remote sensing data.
Bottom temp	[1.7, 18.0]	In Celsius. Average summer bottom temperature*.
Surface salinity	[1.03, 32.4]	In ppt. Average summer surface salinity*.
Bottom salinity	[1.03, 34.7]	In ppt. Average summer bottom salinity*.
Maximum bottom velocity	[0.26, 803]	In cm/s, the maximum bottom tidal velocity*.

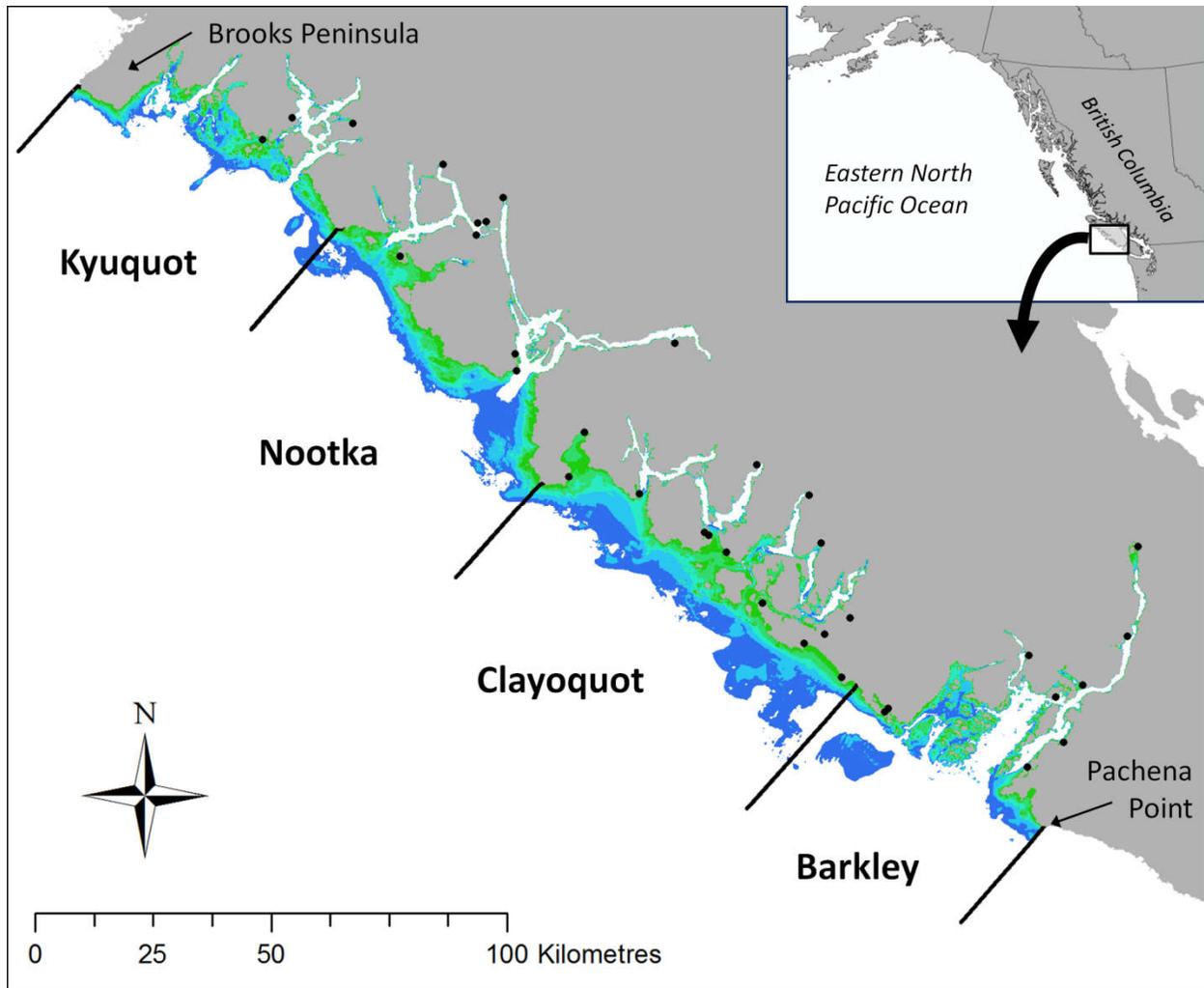
\*From the Foreman Northeast Pacific tidal model (see Foreman et al. 2008 for methods).

Table 5.2: Biomass density ( $g\ m^{-2}$ ) predictions from Ecosim models for Status Quo (SO-) and Laissez Faire (SO+) scenarios, change in biomass density ( $\Delta B = SO+/SO-$ ), and the change ( $\sum Realised\ SO+ / \sum Realised\ SO-$ ) in realised habitat suitability ( $\Delta HS$ ) between the two states. The correspondence distance (CD) is defined as  $(|\Delta B - \Delta HS| / \Delta B)$  and reflects the level of disagreement between the realised habitat model and the biomass model.

Group	SO-	SO+	$\Delta B$	$\Delta HS$	Deviance
Sea otter	0	0.0465	--	--	
Urchin	29.727	0.051	0.002	0.0015	0.08
Dungeness crab	0.065	0	$\sim 0$	$\sim 0$	1530
Geoduck	69.9	52.92	0.76	0.76	0.00
Small clams	19.46	14.01	0.72	0.73	0.01
Lingcod	0.33	0.972	2.95	1.096	0.63
Other rockfish	2.213	3.175	1.43	1.087	0.24
Nereo	16.67	20.32	1.22	1.24	0.02
Macro	12.37	160.7	12.99	2.84	0.78
Other kelp	7.59	36.5	4.81	2.84	0.41

Table 5.3: Fishing mortalities for commercial species.

Group	Fish Mort
Urchin	0.00228
Dungeness crab	1.26
Geoduck	0.00379
Small clams	0.00505
Lingcod	0.0123



*Figure 5.1: Study area showing the regional management areas, the location of coastal communities (black dots) and the study area bathymetry from 0 m (green) to 50 m (blue) depth.*

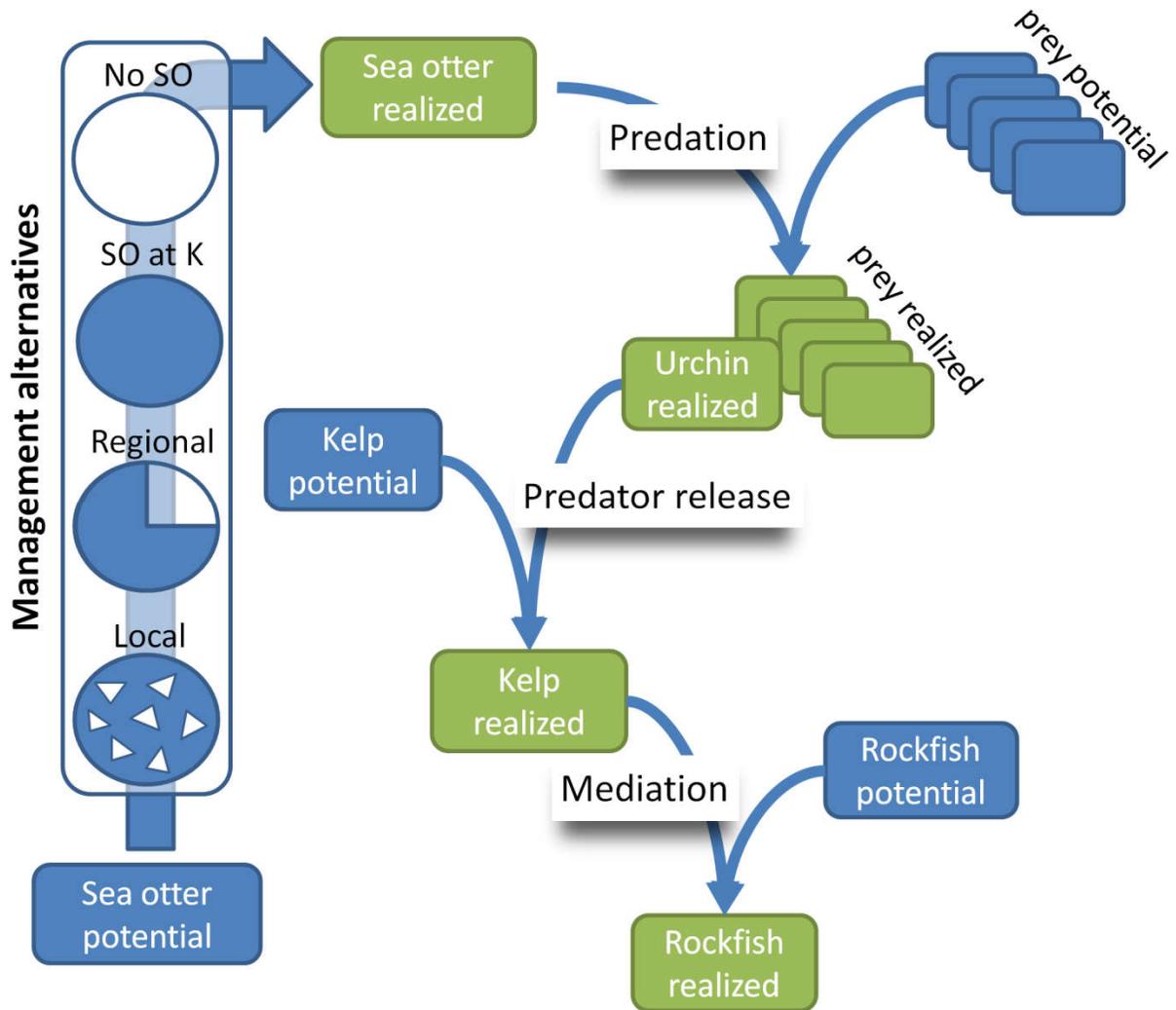


Figure 5.2: The transformation of potential (blue) to realized (green) habitats for the species in the ecosystem model. Realised habitat is defined as potential, abiotic habitat modified by biological interaction. Sea otter potential habitat is transformed by management alternatives; the potential habitats of sea otter prey are transformed through predation; realised kelp habitat is modified through release from predation, which then applies a mediation effect creating enhanced realised habitat for rockfish.

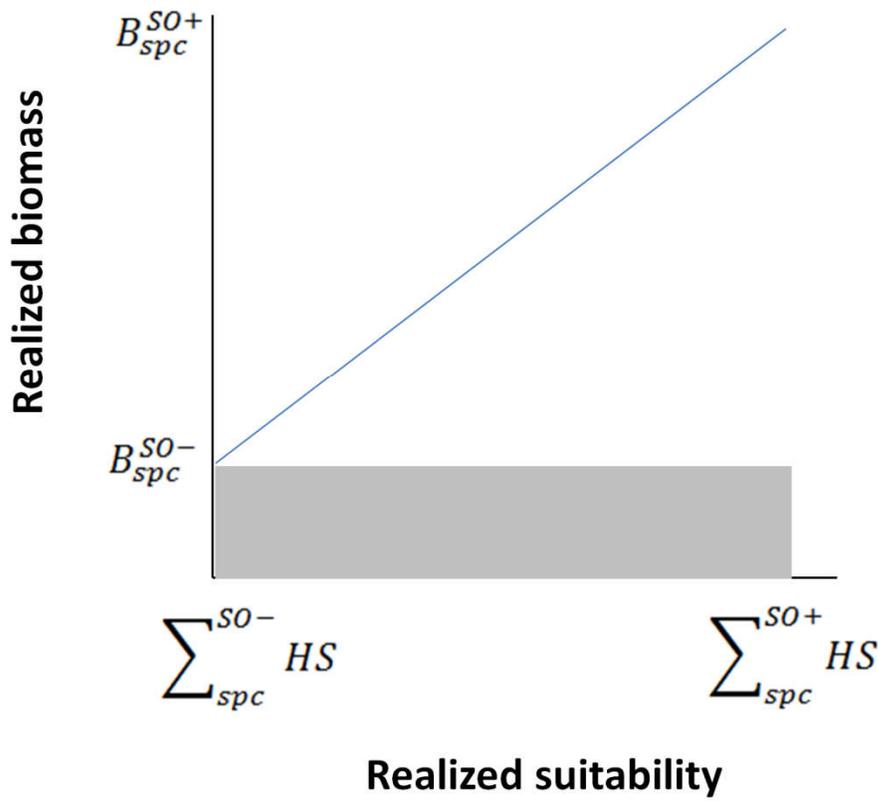


Figure 5.3: Biomass estimation curve used to select the amount of biomass be distributed for each ESP, under each management scenario. The end points of the curve are defined by the sea otter absent (SO-) and sea otter present (SO+) states, with the biomass values obtained from an Ecosim model and the total realised habitat suitability for each state taken from the realised habitat suitability predictions. The shaded area represents the minimum biomass for each ESP, to which an amount is added depending on how much additional habitat suitability exists for each management scenario. This two-step distribution process is necessary to distributing biomass consistently across the management alternatives with the Ideal Free Distribution.

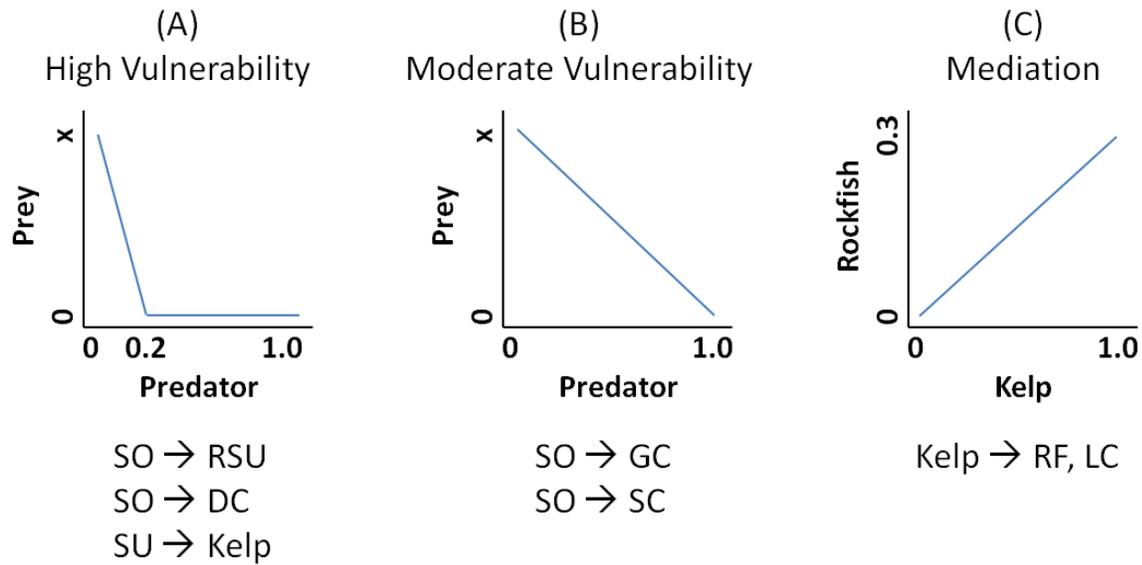


Figure 5.4: Biological interactions used to transform potential habitat suitability predictions to realised habitat predictions. Species with high vulnerability to sea otter predation (RSU, DC) were presumed to be excluded from areas when predator suitability  $\geq 0.2$  (A), while for species with a moderate vulnerability (GC, SC) it was assumed that suitability decreased linearly with predator suitability (B). The enhancement of fish habitat by kelp assumes that suitability is enhanced linearly with realised kelp habitat to a maximum of 0.33. See text for details.

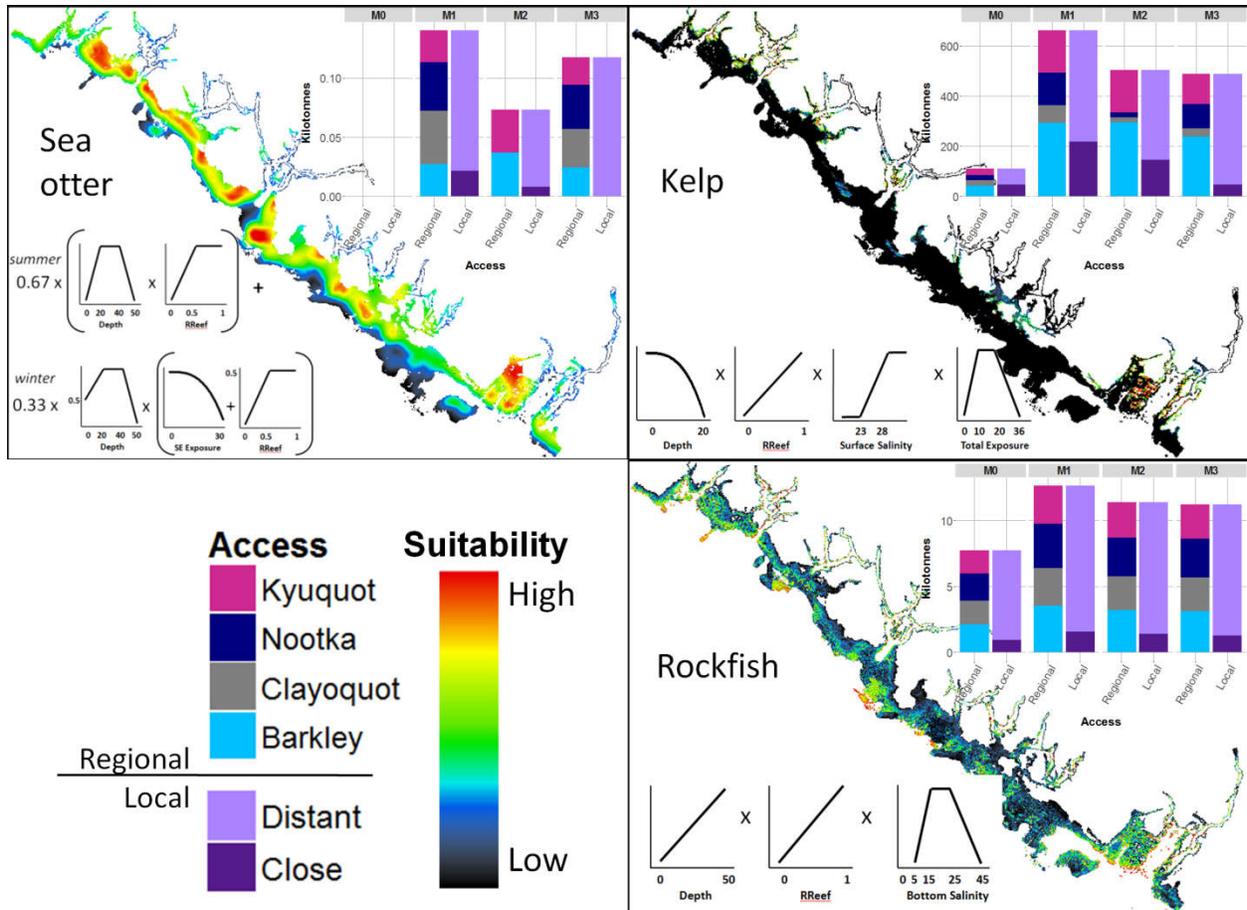


Figure 5.5: Hypothesised habitat suitability models for Sea otter, Kelp, and Rockfish showing the habitat suitability index (HSI) equation and the mapped suitability. Bar graph shows the realised biomass distributions at Regional and Local access levels.

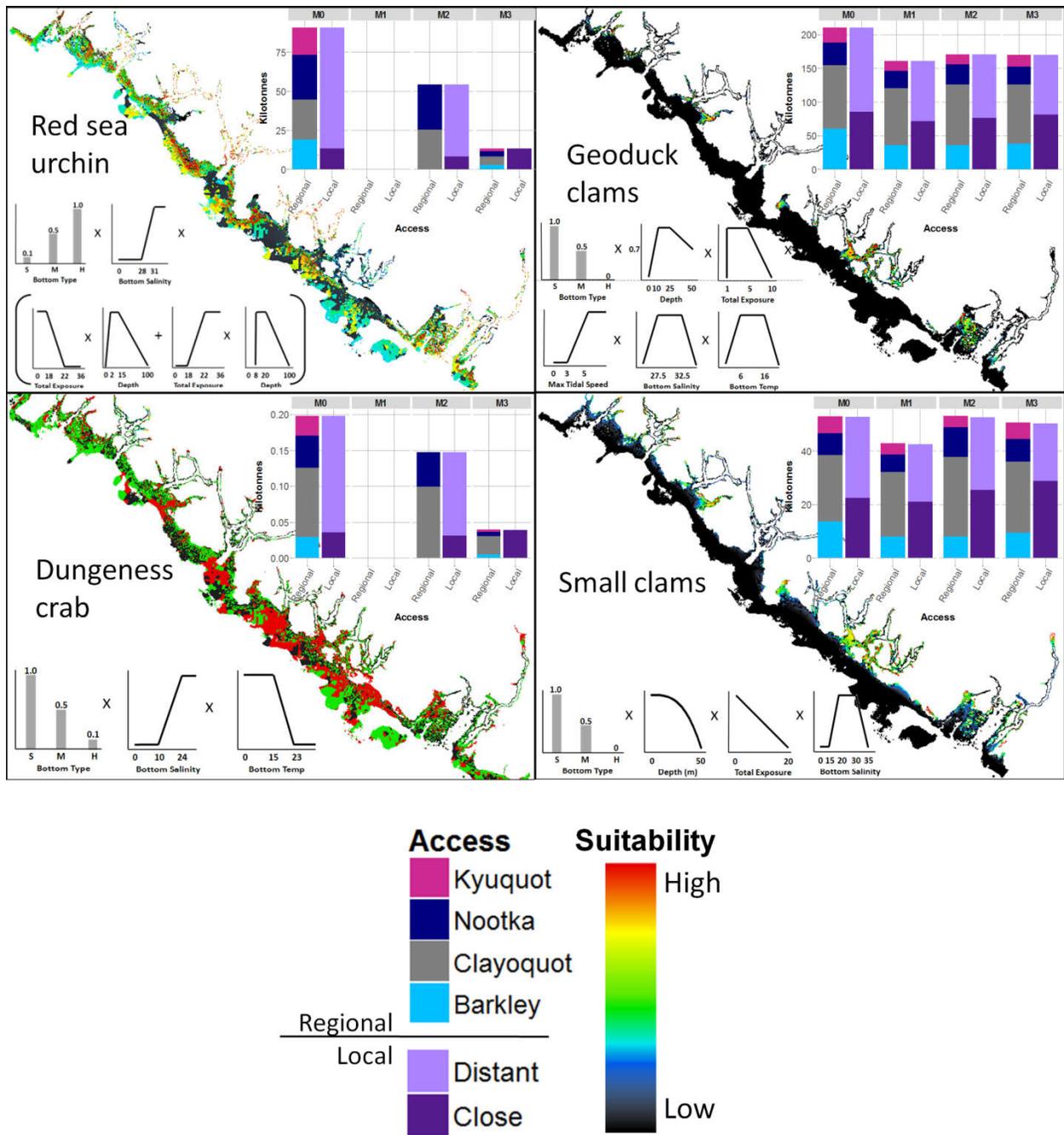


Figure 5.5 (cont'd).

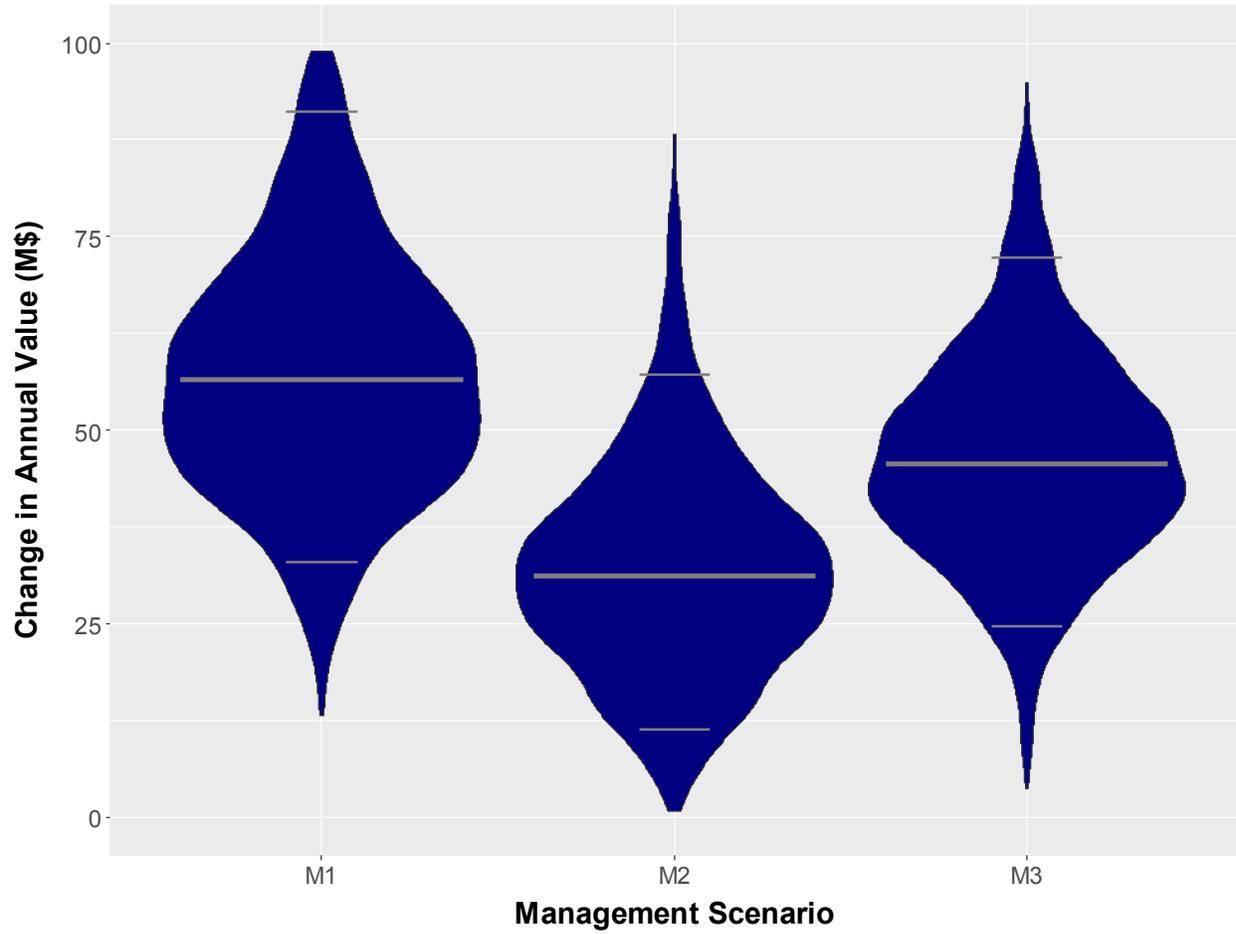


Figure 5.6: Total aggregate change in value (M\$) from baseline (no otters) for the three management scenarios considered.

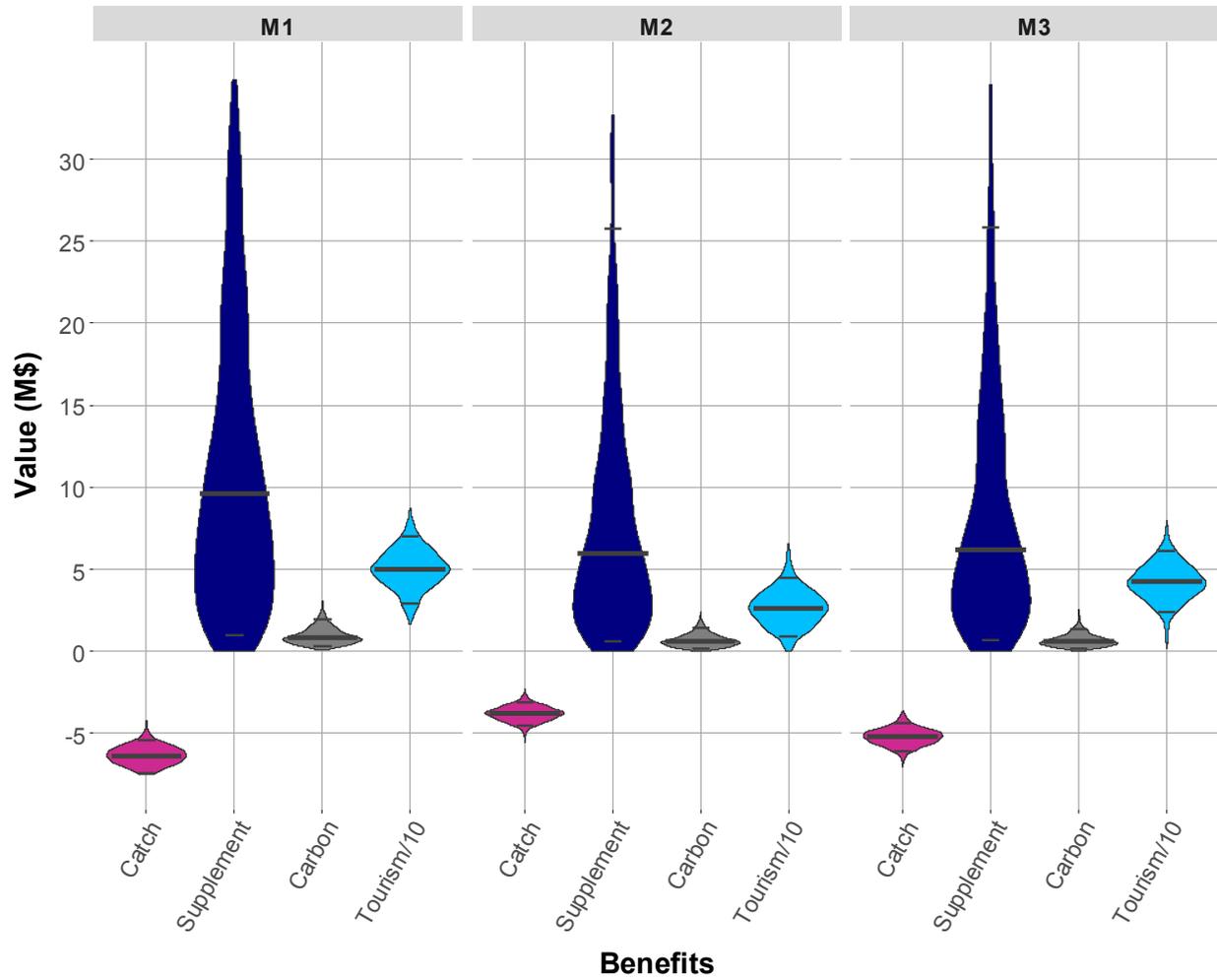


Figure 5.7: Change in individual benefit value (M\$) from baseline for the three management scenarios considered. Note Tourism is /10. Violin plots are trimmed to the extents of data.

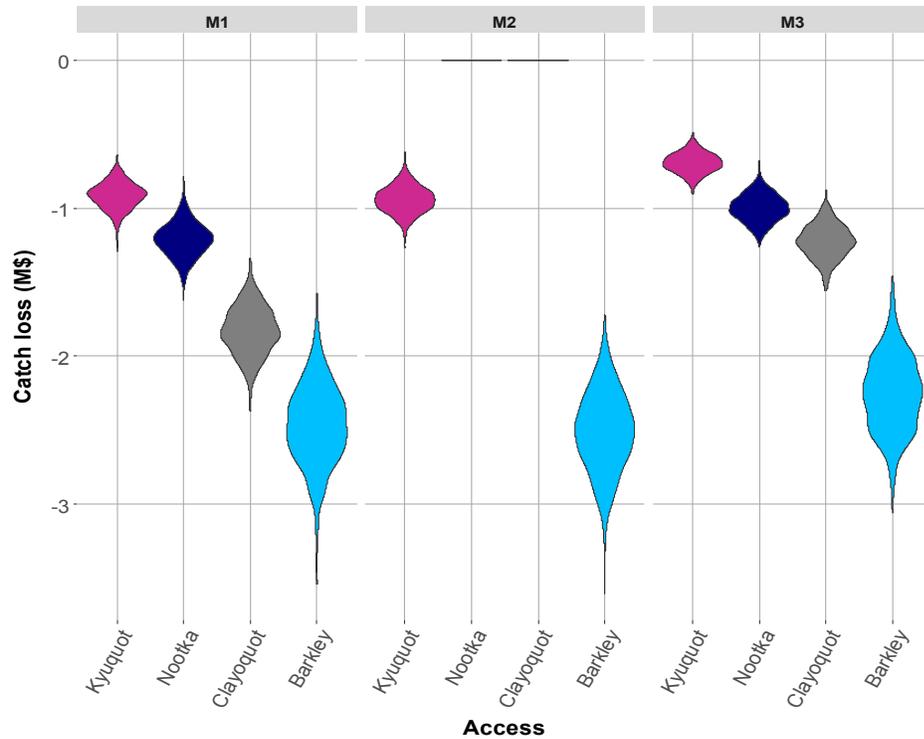


Figure 5.8: Regional cost (M\$) to fishery for each management scenario.

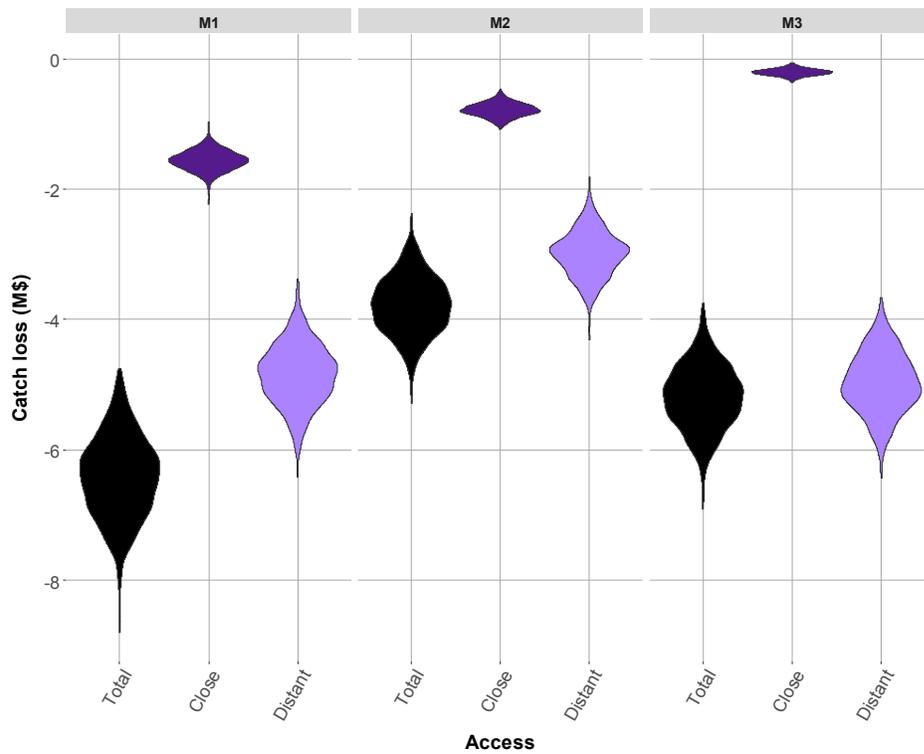


Figure 5.9: Community (Close, Distant) catch loss (M\$) by management scenario. The total catch loss is shown for reference

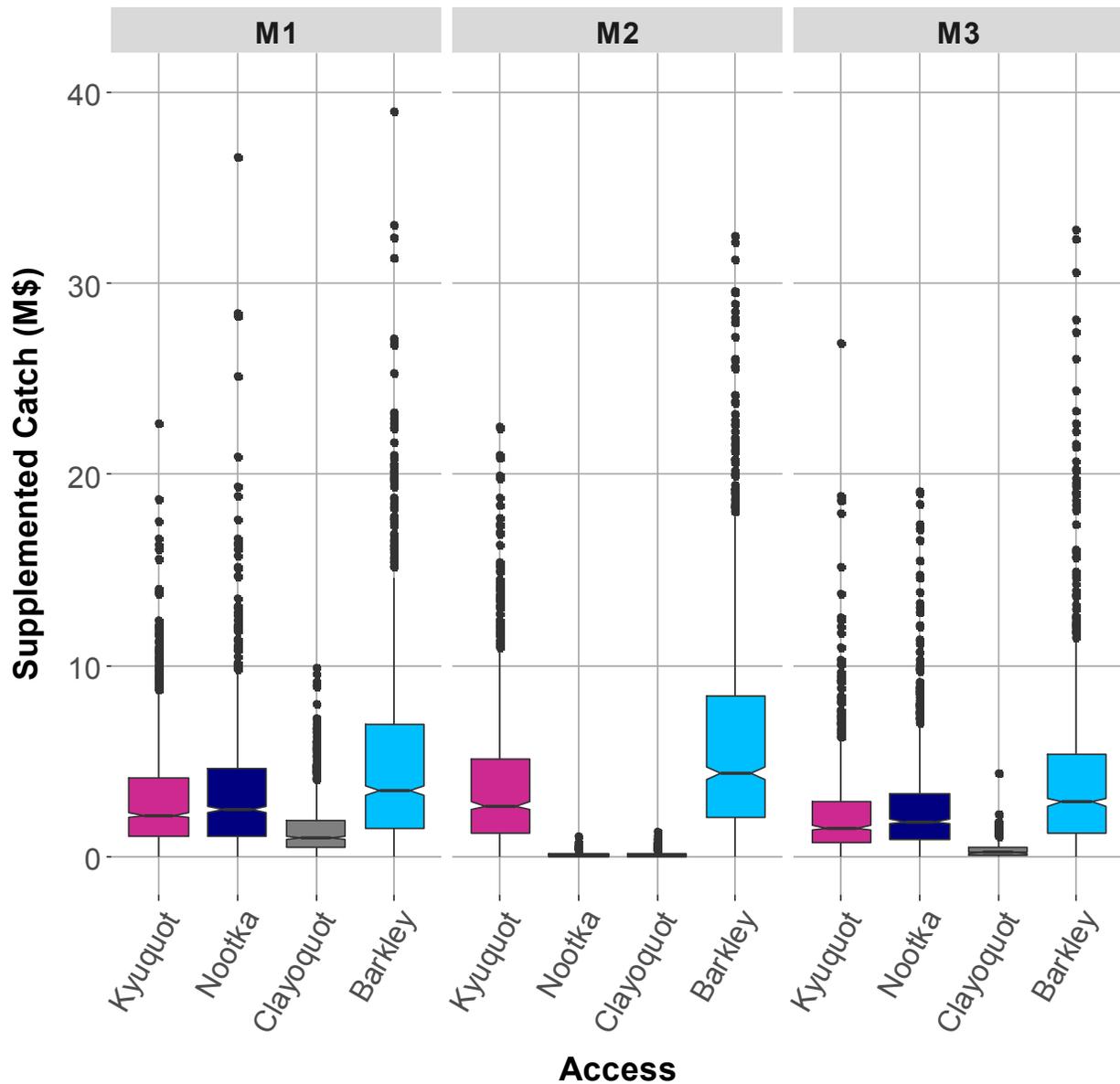


Figure 5.10: Change in value of Supplemented Catch by Region for the different management scenarios shown as box plots with outliers as an example of the range of randomised values generated in this study.

## **Chapter 6 - Conclusions and next steps**

Equitable and sustainable resource management is essential to human well-being. The concept of ecosystem-based management (EBM) frames resource management as an integrated, multi-attribute, multi-value decision making problem. This makes it ideal for evaluating the trade-offs inherent in managing complex social-ecological systems. Such trade-offs are increasingly cast in the language of Ecosystem Services (ES) which relate the benefits realised by people to the ecosystem components that provide them. Ecosystem models are now widely seen as essential to characterising the production of these benefits, and to forecast how they respond to various social and ecological drivers.

However, the design and construction of models intended to support EBM continues to suffer from a range of challenges, fundamentally rooted in the complexity of the systems being modelled. In this dissertation, I have directly addressed three of these challenges: the treatment of uncertainty, the sufficiency of ecosystem models, and the equitable representation of ecosystem service benefits.

I characterised the challenge of uncertainty by reviewing how the most popular ecosystem modelling literature treated uncertainty, and the more fundamental question of defining model scope, including the consideration of assumptions (Chapter 2). I then considered the relationship between the model objective (i.e., the question) and model complexity – an important source of uncertainty. I investigated this relationship by first developing an increasingly complex set kelp habitat suitability models to understand how kelp distribution is related to environmental factors (Chapter 3). I then evaluated the models using independent observational data to illustrate the tension between model complexity and model generality, drawing conclusions about how explicit consideration of objectives could help resolve this tension.

This leads directly to the question of model sufficiency (i.e., how well an ecosystem model serves its intended purpose), which was initially motivated by 1) the many ES analyses that rely largely on marginal estimates of ES production with no consideration of the interactions between the various ecosystem components, and 2) the continued calls for increasingly

complex models to improve our understanding of social-ecological systems. I investigated this question with a case study, using an integrated ecosystem model to address the trade-offs between sea otter recovery and the corresponding losses incurred by commercial invertebrate fisheries in coastal British Columbia, Canada. The model combined field data on a suite of ES providers with population (Chapter 4), habitat (Chapter 5), and ecosystem service models (Chapters 4 & 5). This integration required explicit consideration of assumptions to 1) appropriately scale local data to regional extents; 2) integrate the changes in population with the associated changes in distribution; and 3) translate the distribution of ES providers to services and benefits seen as legitimate by stakeholders.

Explicitly considering such assumptions allowed me to estimate the associated uncertainties (something that is rarely considered in the ES or ecosystem modelling literature, where the focus is more commonly on parametric uncertainties). I combined these design uncertainties with quantitative uncertainty estimates of the model components to create a more comprehensive picture of the overall uncertainty in the integrated model. I used this holistic view of model uncertainty to improve the representation of model credibility, and to bound the complexity of model components based on the overall model precision.

Model sufficiency also depends on the accuracy of the model results and the representation of benefits relevant to stakeholders. I explored this in Chapter 5 by examining how ES distributions were influenced by species interactions, and the translation of potential to realised habitat. I then showed how non-marginal ecosystem changes influence ES production under different management alternatives. The work thus extends both models of social-ecological systems, which generally do not fully account for ESs, and models of ES, which typically allow for only marginal change. I further illustrated the value of spatial resolution by showing that ES production could be aggregated to represent rarely considered benefits, such as equity of access.

### ***Findings***

My review of the most popular marine ecosystem modelling papers (Chapter 2) showed how different disciplines have approached the challenge of model scope from three distinct

perspectives, leading to models that focus principally on either the temporal or spatial aspects, or on the richness of the representation. This reductionism is a necessary part of making models of complex systems tractable, and has led to significant advances in representation of populations, habitats, and services. However, the review also showed that the treatment of model assumptions and uncertainty is generally quite poor, at least in the most popular articles. Thus, the answer to my first research question, *Does the treatment of uncertainty in the ecosystem modelling literature provide enough information to assess model credibility?*, is an emphatic "No". To help make assumptions underlying model design decisions more explicit, I proposed a conceptual model to help articulate the assumptions needed to abstract our models from their ecological context across temporal, spatial, and richness dimensions. I also defined a typology of the assumptions (and their associated uncertainties) typically used to make ecosystem models tractable.

The kelp habitat model developed in Chapter 3 yielded a number of insights into how abiotic factors contribute to kelp habitat suitability including the previously undescribed roles of salinity and interactions among predictors. This effectively answered the first part of my second research question - *What determines good kelp habitat?* The second part of this research question, *How well can we predict it?*, was answered by my independent data evaluation of model performance which showed the potential for over-fitting by correlation-based (e.g., statistical) models, and identified how temporal bias in the dependent data can influence the quality of the model prediction. Finally, I answered the third part of this research question, *Is there a difference in the performance of correlative vs. process-based models of habitat suitability?*, by comparing the forecasting skill of correlative models with that of simple, ecologically informed process-based model. While the process-based model was not as good as the correlative ones at predicting a particular set of observations, it did perform as well or better when confronted with independent data.

My next research question, *What is the difference in ES benefits between otter-present and otter-absent systems on the West Coast of Vancouver Island, BC?*, is answered in Chapter 4. My ecosystem model realistically represented the sea otter induced trophic cascade, and illustrated

that while the losses to invertebrate fisheries may be substantial, particularly for sea urchins and Dungeness crab, these losses would likely be offset by the benefits arising from increases in finfish abundance. Wildlife tourism was predicted to have the highest potential value, while a notable increase in carbon sequestration also contributed to the value of the otter-present system. I defined a simple, accessible representation of the integrated uncertainty, facilitated by the finding that the translation of ecosystem service supply to benefits was far greater than the parametric uncertainty in the model of ES production.

In Chapter 5, the integration of the habitat models with the population model from Chapter 4 directly addressed my fourth research question, *Does understanding the spatial distribution of ES provision influence the ranking of management alternatives?* This analysis showed that mapping the distribution of ES can influence the ranking of management alternatives in two ways. First, mapping fungible services at the appropriate spatial resolution enabled indicators of benefit (i.e., accessible resources) to be developed. Second, spatially resolved benefits can uncover a range of non-fungible social and ecological benefits allowing a more comprehensive assessment of possible management alternatives. Methodologically, the translation of potential to realised habitat led to the identification of a metric to measure the agreement between predicted change in population and habitat arising from species interactions. This metric, termed the correspondence distance, has the potential to be used to evaluate the relative performance of different habitat suitability models.

### ***Significance and contributions***

While perhaps unlikely to surprise many in the field, the finding that model design and uncertainty are poorly treated in the literature are significant because they illustrate the pervasiveness of a largely undocumented problem. Likely causes include institutionalized disregard of reproducibility for the benefit of conciseness, a low tolerance for quantitative detail by many scientists, and a general misunderstanding of model design principles. This has real consequences for the utility of ecosystem models for management, since without a clear question, and at least some consideration of uncertainty and model credibility, managers have no way of assessing the value of the predictions from such models.

A misunderstanding of model design principles is likely a big part of why understanding is often given precedence over, or conflated with, defining management objectives, thereby compromising the effective and timely application of models for resource management. The unified view of model scope (articulated in Chapter 2 by integrating the domains of the 3 disciplines contributing to ES mapping) offers a perspective on model design that can help modellers, stakeholders, and managers understand the complexity of the decision context and the consequences of different scaling decisions. I hope this emphasis on model scope, and on driving model design with the management question rather than ecological understanding, will lead to more robust, purpose-built models for management. It is important to note that this focus on model sufficiency does not undervalue models for understanding, which are essential for improved model accuracy and precision. Rather, the expectation is that by disentangling the two objectives, ecosystem models can become more relevant to both.

The use of independent data to evaluate increasingly complex model predictions illustrates how the trade-off between developing models for understanding vs. application can be quantitatively managed. While the benefits of using independent data to validate model forecasts are widely understood, this novel application represents a significant contribution because it provides a way to identify models whose complexity may compromise their utility to decision support. The analysis is also useful as a reminder that simple, ecologically sound models have a role in forecasting species distributions, especially in data-poor contexts, and in situations where timeliness prohibits the use of more complex, data-hungry methods. The illustration of temporal bias (i.e., the anchoring of correlation-based models to the time period when the data are collected) is also significant, and critical to forecasts of future distributions which can be strongly influenced by initial conditions.

While ecosystem models do require sufficient complexity to realistically represent the social-ecological system of interest, attempts to increase model relevance have tended to lead to increased complexity. Fortunately, the integrated model presented in Chapter 5 shows that limits on this complexity can be found by considering the full range of uncertainties in the integrated model, including that in our assumptions, as well as what can be measured more

quantitatively. This relies on a holistic comparison of the most significant model uncertainties to identify where complexity can be reduced with little or no cost to the accuracy of the integrated model. This conceptual framework for limiting the complexity of model components given greater uncertainties elsewhere in the model represents an important advance in identifying model sufficiency. This broader consideration of uncertainty also enables a novel representation of the overall model credibility using the dominant uncertainties rather than the more typical approach of representing component uncertainty. This has the potential to greatly improve how uncertainty in ecosystem models is communicated, significantly increasing the potential utility of models to management.

The importance of mapping marine ES production is illustrated by its role in the ranking of management alternatives, and is of crucial importance to effective EBM of marine systems. Such spatial representation allows social benefits like equity of access to be represented, enhancing the appropriateness and legitimacy of the management exercise. Access-based estimates of ES benefits also align model scope more closely with societal and management needs. This increases legitimacy and broadens the alternatives available to managers, making this advance an important contribution to the utility of ecosystem models.

The application of this modelling approach to the resource conflict on the west coast of Vancouver Island is the first quantitative comparison of ecosystem services in this dynamic coastal ecosystem, and provides critical information about the trade-offs in this and similar ecosystems. The analysis emphasises the importance of representing realised (as opposed to potential) habitat when considering spatial management alternatives, and illustrates the potential for maximising overall benefits by aligning them strategically with where they are most abundant.

Collectively, my dissertation offers applied, theoretical, and methodological advances for models of social-ecological systems. The integrated ecosystem model provides the first regional analysis of benefits and costs of the sea otter trophic cascade in the eastern North Pacific; and the kelp model illustrates how model objectives can inform both model complexity and utility. Theoretically, the design of the integrated model gives insight into how a more explicit

understanding, representation, and treatment of uncertainty results in both a means of determining sufficient model complexity, and an avenue for a more comprehensive, digestible representation of model uncertainty. Methodological advances include a conceptual framework and assumption typology for supporting model design, a novel application of independent data evaluation, and a method for evaluating the potential habitat suitability models necessary for species-mediated translation into realised habitat.

### ***Limitations and next steps***

As implied in Chapter 2, the most realistic ecosystem model may be a fully dynamic integration of the social-ecological system of interest. However, despite the availability of tools to develop such models, our ability to credibly parameterise the many ecological and socio-ecological dynamics remains severely limited (e.g., Joppa et al. 2016). Assuming ecological processes are stationary is thus a staple (albeit a largely implicit one) in the ecosystem modelling and mapping literature, leading to models that can consider only marginal ecosystem changes, even if uncertainties are represented. Transparent methods to identify when this widely applied assumption of stationarity ought to be rejected would provide more consistent methods of defining spatial and temporal scale.

Alternate state models such as the one developed here or by climate change ecologists (e.g., Cheung et al. 2009) are a step in the right direction. Such coupled models provide a reasonable alternative to dynamic models and allow models with similar levels of complexity to be combined. However, this comes with a need to evaluate the confidence that should be placed in the individual model components, as well as the linkages between them. While I addressed a number of these uncertainties in the development of my integrated model, a more thorough examination of my claim that I represented the greatest uncertainties would be warranted before adopting the model for management.

More specifically, the potential habitat suitability models represent one source of potential refinement, particularly in light of the high correspondence distance (see Chapter 5) for some species. Revisiting these models and examining whether changes to the habitat suitability can

improve this metric would likely improve overall model accuracy, while further developing what is potentially a valuable new tool for integrated model validation.

My representation of several ES benefits was somewhat simplistic, as was my treatment of access. The tourism benefit could be refined with data on infrastructure and assumptions about tour operator behaviour. The value of both the catch loss and supplemented finfish services could be elaborated with the inclusion of services and benefits beyond landed value. A more precise representation of access could be achieved with data on demographics, refining the various equity trade-offs. These could be further augmented by considering a range of other values that people associate with ecosystems and their relationship with those systems (e.g., relational values; Chan et al. 2016). Nevertheless, despite these obvious limitations, the core findings of the analysis regarding trade-offs between aggregate value and the role of space in defining realised benefits and novel indicators of equity are robust to these simplifications. In fact, the explicit consideration of uncertainties and the inclusion of a credibility estimate serve to illustrate a key point of my dissertation – that sufficient model complexity can be estimated based on the question being asked.

Explicit representation of the decision context, including stakeholder values and objectives, would also significantly advance the utility of this model. Integrating stakeholder values is a significant undertaking (e.g., Fulton et al. 2015), however a reasonable step in that direction would be to prototype a decision model using past decision support work in the study area (Espinosa-Romero et al. 2011a). This data-to-decision integration would allow the model to inform a structured decision-making analysis, and the interaction between model uncertainty and confidence in decision-making to be explored. This elevation of model uncertainty to the decision context would round out assessments of model sufficiency: by examining how the various uncertainties effect stakeholder utility, the costs of reducing that uncertainty could be estimated using value of information analysis (Canessa et al. 2015) and help determine whether the model is sufficient for the management question at hand.

Ecosystem models may also benefit from efforts to further categorise both the biotic and abiotic components. For example, combining similar species into functional groups is a

cornerstone of Ecopath models, and has met with considerable success. Similarly, classifying life-history processes among taxa (e.g., Kindsvater et al. 2016) may help manage the complexity of ecosystem dynamics, while classifying habitat according to functional traits (e.g., Gregr et al. 2016) may simplify habitat associations. Kindsvater et al. (2016) claim that understanding life history–environment interactions is integral to sustainability. I would add that such insights are also essential to tractable representations of ecosystem dynamics.

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## Appendix 1 - Ecosystem model functional groups, parameters, and technical results

### Overview

This appendix describes the species groups used in the West Coast Vancouver Island (WCVI) Ecopath and Ecosim models, how the Ecopath parameters were derived, and how the necessary parameters were adjusted during model balancing. The rationale used to parameterise the Ecosim dynamics, including Mediation and Vulnerability, is also described.

The study area (3043 km<sup>2</sup>) included all sea otter foraging habitat from Brooks Peninsula to Pachena Point on the WCVI from the lower water line to the 50 m depth contour, including both hard and soft bottom types. Hard substrates were estimated to comprise 30% of the study area, based on Gregr et al. (2008). Estimates of species biomass needed to be scaled according to the proportion of their potential habitat within the study area. For example, giant kelp (*Macrocystis pyrifera*) is limited to depths of 20 m or less. This depth range covers roughly 30% of the study area. Combined with the 30% hard substrate assumed suitable for kelp attachment give  $0.30 * 0.30 = 0.09$  or about **10%** of the study area that can be considered potential kelp habitat. However, in the otter-absent state, the *realised* proportion of this potential habitat is reduced - extensively in some cases - because of species interactions (e.g., grazers, most notably sea urchins). Nevertheless, this 10% habitat assumption is used as the starting point for scaling data for kelp and kelp associated species. For infaunal invertebrates, it was further assumed that 30% of the study area is soft bottom.

Such estimates, assumptions, and considerations form the basis of scaling observational data from local studies to regional biomasses, as required for management-scale ecosystem models. Estimates of biomass (B) for ecosystem models must consider both the abundance of the group of interest within its habitat, and the proportion of that habitat within the study area. This is particularly important for sessile species (e.g., bivalves, macroalgae) and those closely associated with particular habitat types (e.g., rockfish). Thus, estimating B from abundance surveys, typically conducted in suitable habitat, requires some consideration of how suitable habitat is distributed within the study area.

This model includes 24 species or functional groups (Table A1). These groups include sea otters and their main prey species, as well as trophically related commercial species. For each group, the rationale underlying its parameterisation is described.

With respect to diet composition, because randomisation was used to explore the uncertainty around the parameters, and the randomisation does not add new groups to the diet, diets were defined as broadly as reasonable to allow the randomisation to search widely for potential diet combinations rather than impose a more restrictive diet *a priori*.

### ***Initial parameter estimates***

Parameters for biomass ( $B$ ,  $\text{g m}^{-2} \text{yr}^{-1}$ ), production per biomass ( $P/B$ ,  $\text{yr}^{-1}$ ), and consumption per biomass ( $Q/B$ ,  $\text{yr}^{-1}$ ) for the groups in the model (Table A2) were 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, Harvey et al.'s (2010) recent analysis of an ecosystem with many of the same species and groups was broadly consulted.

The diet of each species is also described (Table A3), including both the prey and predators considered in this model. Species and group abbreviations are noted when each species is introduced. These and other abbreviations used throughout are summarised in Table A1.

#### *Sea otters (SO)*

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

*Biomass:* In the Otter-absent model,  $\mathbf{B} = \mathbf{1e-6} \text{ g m}^{-2} \text{yr}^{-1}$  was used as a placeholder for the subsequent reintroduction biomass. To then seed the population recovery and generate the otter-present state,  $\mathbf{B} = \mathbf{5.085e-4} \text{ g m}^{-2} \text{yr}^{-1}$  was calculated as the biomass of sea otters introduced in 1970 (based on 89 animals with mean weight of 20 kg (Williams 1989) in a study area of 3043  $\text{km}^2$ ).

*Production:* The initial population growth rate ( $P/B = 0.186 \text{ yr}^{-1}$ ) was taken from Watson et al. (1997).

*Consumption:* Sea otter  $Q/B$  was estimated using the midpoint (28%) of the daily ration (23-33% of body weight) reported by Riedman and Estes (1990). This gave an annual consumption rate of  $0.28 * 365 = Q/B = 102.2 \text{ yr}^{-1}$ .

*Diet:* SO diet composition (Table A3) was based largely on Laidre and Jameson (2006) who described a diverse diet in areas where otters were established (Northwest coast of Washington state), and a more limited diet in a newly occupied area (South side of Juan de Fuca Strait). In Juan de Fuca Strait, based on frequency of occurrence, they found the sea otter diet dominated (70%) by sea urchins (*Strongylocentrotus* spp.) with the balance (~25%) comprised mainly of large bivalves. In contrast, the diet on the Northwest coast 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, but including LGs, SIs, and small amounts of other invertebrates (i.e., MU, OEC, KC, and PI) was used in the model to allow adjustments in diet based on changing prey abundance.

#### *Sea urchins (SU)*

This group (*Strongylocentrotus* spp.) includes red, purple, and green sea urchins. Red sea urchins are the largest of the 5 urchin species found in BC. They inhabit rocky substrate mainly from the intertidal zone to 50 m, though individuals can be found to 125 m. (DFO 2011). The smaller green and purple urchins have similar ranges and diets, but are less important commercially.

*Biomass:* Previous models of the study area have used B values ranging from 6.7 to  $30 \text{ g m}^{-2} \text{ yr}^{-1}$ . Campbell et al. (2001) reported average densities (1.11 and  $2.011 \text{ m}^{-2}$ ) and average biomass of harvestable red sea urchins (> 90 mm) from 2 statistical area in Clayoquot Sound as 455.29 and

669.92 g (mean = 562 g m<sup>-2</sup>). This is well less than the potential maximum densities (2.67 urchins m<sup>-2</sup>) and biomasses (1204.07 g) reported for this, and other nearshore systems.

For example in the western North Atlantic, urchin B in urchin barrens is reported in the range 1100 - 1200 g m<sup>-2</sup> (Scheibling 1986). In BC, Watson and Estes {Watson, 2011 #1942} report B values from rocky reefs in Barkley Sound ranging from 2800 to 3400 g m<sup>-2</sup>, and show pre-otter densities in Kyuquot declining from a maximum of 2900 g m<sup>-2</sup> to as low as 25 g m<sup>-2</sup> 30 years after sea otter introduction. Data collected as part of the BC Coastal Ecosystem Services (BCCES) project estimated 1500 g m<sup>-2</sup> for Barkley Sound. Thus, while there is a potential for very high 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 SU from Kyuquot were used to represent the change in B between otter-absent and otter-present areas. Since SU are found almost exclusively on rocky reefs, the B value was scaled using the 30% rocky reef assumption, and an additional assumption that only 30% of rocky reefs were suitable oceanographically. This 10% habitat suitability assumption yielded an estimated **B = 290 g m<sup>-2</sup> yr<sup>-1</sup>** for the study area in the otter-absent state, and **B = 2.5 g m<sup>-2</sup> yr<sup>-1</sup>** in the otter-present state (Table A2).

*Production:* SU reproduction is poorly understood, however recruitment events are believed to be infrequent when populations are high (Pearse and Hines 1987). Following Brey (2001, 2012), an estimate of SU P/B was calculated from individual weight and various life history characteristics (Tables A4 and A5). Average individual wet weight was obtained from a growth equation and the mean test size (79.2 mm) of pre-sea otter SUs reported by Watson and Estes (Watson and Estes 2011). The growth equation gave a mass of 186 g, and the Brey method calculated a **P/B = 0.2438 yr<sup>-1</sup>** (Table A5). This value is likely an under-estimate as it does not consider the higher P/B of the shorter-lived green urchin (Harvey et al. 2010).

*Consumption:* Harvey et al. (Harvey et al. 2010) estimated SU consumption as **Q/B = 10.88 yr<sup>-1</sup>** based on laboratory consumption rates (McBride et al. 2004). This value was adopted here, while recognising that a lower value may be more appropriate in a nutrient limited environment such as an urchin barrens.

*Diet:* 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 (Rowley 1990). Green urchins are known to actively climb and feed on live kelp (Harvey et al. 2010). For lack of additional information on diet or relative abundance of green and red urchins, a diet of equal parts Nereo, Macro, OM, and KD was assigned. A higher proportion of KD may be warranted in urchin barrens, where SU are less active grazers, preferring to passively wait for KD (Konar and Estes 2003).

#### *Large commercial crab (LCC)*

Dungeness crab (*Metacarcinus magister*) is the second most valuable invertebrate in Pacific Canada (Province of British Columbia 2014) and is by far the dominant species in this group. 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 species of crab (Pacific rock - *Cancer antennarius*, and red rock - *Cancer productus*) are caught commercially, however catches are small compared to Dungeness. Parameters for this group are drawn primarily from Dungeness crab literature since there is less data on the lower valued species. However some attention is paid in the diet to the other species which are considered to be more predatory.

*Biomass:* DFO stock assessments provide an average weight of LCC caught (740 g/crab; DFO 2000), but no published abundance estimates for Pacific Canada were found, likely because the fishery is conservatively and effectively managed using size and sex restrictions (DFO 2000). The only available data on density was obtained from a multi-year study in the Columbia River estuary (McCabe Jr. et al. 1988). These data illustrate the high inter- and intra-annual variability in crab densities, making such direct measures difficult. Therefore, following Harvey et al. (2010), Ecopath was allowed to estimate **B** based on a presumed EE = 0.90.

*Production:* LCC was assigned a **P/B = 1.50 yr<sup>-1</sup>** based on the average from two source models of the study area (Ainsworth et al. 2002, Preikshot 2007). This corresponded well with the value estimated by Harvey et al. (2010).

*Consumption:* LCC was assigned a  $Q/B = 4.25 \text{ yr}^{-1}$  based on the average from two source models of the study area (Ainsworth et al. 2002, Preikshot 2007). This corresponded well with the value estimated by Harvey et al. (2010).

*Diet:* Crab are often viewed as opportunistic predators, with the diet described as containing a variety of crustaceans, bivalves, polychaetes, juvenile fish, and algae (e.g., Stevens et al. 1982). However, such studies are based on stomach contents, and often conducted in estuaries. Observed diet diversity may be due to active predation, or scavenging (i.e., detritus). While it is reasonable to envision LCC preying on sessile invertebrates, it is harder to imagine LCC capturing highly mobile fish species. In particular, the implication that LCC prey on forage fish (Harvey et al. 2010, Stevens et al. 1982) seems tenuous. Here, LCC diet is focused on invertebrates, and is dominated by SI (0.34), followed by Detritus (0.25) and shellfish (OEC and MU assigned 0.10 each). The remaining diet was divided equally among SU, KC, PI, LG, and SG, with just 0.01 assigned to cannibalism (Table A3).

#### *Edible bivalves*

To capture the commercial provisioning services of the functional groups, Edible Bivalves were divided into 3 groups: Geoducks, Mussels, and Other Edible Clams. Japanese oysters (*Crassostrea gigas*) were excluded from the model because, while an important species for human consumption, it is not a principal prey item of sea otters.

*Diet:* The diet of these 3 groups was assumed to be similar, comprised largely of particulate organic matter (POM). However, since POM was not explicitly represented in the model, assumptions about the proportions from potential POM sources (this can include early life history stages of some species) were also needed. In an otter-absent state, most of the POM is assumed to come from Primary Production (PP, 0.78) with contributions from both Kelp detritus (KD, 0.10) and Detritus (D, 0.10). A small possibility (0.01) of drifting LZ and SH groups as also considered (Table A3). B, P/B, and Q/B are described for each group below.

### *Geoduck clam (GC)*

Geoduck clams (*Panopea generosa*) are the most valuable commercial invertebrate fishery in Pacific Canada (Province of British Columbia 2014). Within the study area, commercial harvest is highest in Clayoquot Sound, but significant fishing (including horse clams) occurs throughout the study area (BCMCA 2010). Geoducks are found from the ITD to depths of 100 m (Goodwin and Pease 1991), however dive harvesting occurs entirely within the study area, in depths less than 20 m. Besides humans and SO, they have no known natural predators as adults. Predation during larval and early-burrowing stages are presumed to be similar to other species with a larval and settlement life history.

*Biomass:* Species-specific parameters from stock assessments (DFO 2011) were used to estimate **B** for this group. Mean GC weight in the study area is reported as 1.0 kg, with wild densities ranging between 0.54 and 0.86 per m<sup>2</sup>. This suggests a B between 540 and 860 g m<sup>-2</sup> in suitable habitat. This is considerably lower than the observed bed density of 1590 g m<sup>-2</sup> in Southeast Alaska (unpublished data), suggesting GC densities (perhaps driven by habitat suitability) are highly variable. The mid-point of the BC estimate was scaled to the study area by combining the 30% soft bottom assumption with an additional 30% oceanographic suitability assumption giving a 10% habitat suitability. This scaled the 700 g m<sup>-2</sup> midpoint to a **B = 70 g m<sup>-2</sup> yr<sup>-1</sup>**. This not much more than Harvey et al.'s (2010) estimate of 52.4 g m<sup>-2</sup> which they describe as conservative.

There is some uncertainty around the impacts of SO on GC. Anecdotal reports from fishers suggest the reduction of GC density in otter-present areas is significant. However, this has yet to be borne out by the data. Reidy and Cox (2012) found no difference in GC density between groups of sites with and without SO, although this appears to have been confounded by significant inter-annual variability. While in Southeast Alaska, the ratio of mean GC B between surveyed beds with and without otters is 0.87, with a concurrent reduction in the size distribution (unpublished data). A factor of 0.80 was therefore used to estimate a **B = 56 g m<sup>-2</sup> yr<sup>-1</sup>** for otter-present areas (Table A3).

*Production:* Following Harvey et al. (2010), the estimated exploitation rate (1.2% - DFO 2011) was added to the mean ( $0.036 \text{ yr}^{-1}$ ) of a recently estimated natural mortality of between 0.014 and  $0.054 \text{ yr}^{-1}$  (Reidy and Cox 2012) to arrive at a **P/B = 0.048**  $\text{yr}^{-1}$ , in line with the  $0.036 \text{ yr}^{-1}$  used by Harvey et al. (2010). This is considerably less than the  $0.125 \text{ yr}^{-1}$  estimated according to Brey (2012) (Table A5), suggesting the value could be somewhat low.

*Consumption:* A **Q/B = 2.0**  $\text{yr}^{-1}$  was taken from Harvey et al. (2010).

#### *Mussels (MU)*

Mussels (*Mytilus californianus*) occur attached to hard substrate in highly exposed areas of the coast. This is in contrast to *Mytilus edulis* (described in Harvey et al. 2010) which prefers relatively protected estuarine bays.

*Biomass:* Singh et al. (2013) estimated a remarkable  $B = 82,600 \text{ g m}^{-2}$  in suitable habitat from field surveys. In otter-present areas, these values were lower (**B = 57,100**  $\text{g m}^{-2} \text{ yr}^{-1}$ ).

To scale this sizable biomass to the study area, and bring it more in line with the other bivalve groups, it was arbitrarily and likely conservatively assumed that suitable MU habitat 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**  $\text{g m}^{-2} \text{ yr}^{-1}$  for otter-absent areas. In the absence of assessments of MU habitat suitability, the reasonableness of this assumption is difficult to assess. However, the value is in line with the other groups in the model, and lower biomasses are generally necessary for predation to influence the B of the group.

*Production:* P/B was estimated using empirically-based allometric models provided by Brey (2001, 2012) to estimate energy per individual (Table A4), and then calculate P/B using energy and life history characteristics (Table A5). For MU this gave an estimated **P/B = 0.428**  $\text{yr}^{-1}$ .

*Consumption:* Following Harvey et al. (2010), I estimated **Q/B = 1.42**  $\text{yr}^{-1}$  by dividing the P/B estimate (above) by a presumed bivalve growth efficiency of 0.3.

#### *Other Edible clams (OEC)*

Five commercial species of clams are found in the AOI including Manila (*Venerupis philippinarum*), littleneck (*Protothaca staminea*), butter (*Saxidomus giganteus*), razor (*Siliqua patula*), and varnish (*Nuttallia obscurata*) clams. For this purposes of this analysis, This 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 (DFO 2013). Butter clams also serve as an important prey item for SO in southeast Alaska (Kvitek et al. 1993). Clams are managed by area, within which subareas correspond to fishery management areas. Several beaches in area 23 (Barkley) and 26 (Kyuquot) now closed to harvest as set-asides for FN FSC purposes (DFO 2013).

*Biomass:* A method for estimating B was derived using species-specific parameters from DFO stock assessments, and other related references. The method first assumed that harvest reference points described suitable habitat densities. The DFO Integrated Fisheries Management Plan (IFMP) (DFO 2013) describes a harvestable reference point of 30 legal size clams per m<sup>2</sup>, although densities can be in excess of 130 legal per m<sup>2</sup>. Legal sizes are: littlenecks (38 mm), butter (63 mm), manila (68 mm) and razor (90 mm).

The legal lengths were converted to weight based on an allometric (length-weight) growth model (Bradbury et al. 2005) (Table A6). 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 3 species were converted to densities using the harvestable density reference points and summed the species minimum legal densities (30 per m<sup>2</sup>) to generate a conservative estimate of total **B = 6462 g m<sup>-2</sup> yr<sup>-1</sup>** in suitable habitat areas.

To scale this B for the study area, the 10% soft bottom assumption was combined with the assumptions that only 30% of the study area have suitable water chemistry, and that OEC habitat extends over only 10% of the model depths (assuming uniform depth distribution and a maximum 5 m depth for OEC habitat). This gives an estimated habitat scaling factor of (0.1\*0.3\*0.1) giving a potentially conservative **B = 19.39 g m<sup>-2</sup> yr<sup>-1</sup>** for the study area.

*Production:* Harvey et al. (2010) estimated  $P/B = 2.059 \text{ yr}^{-1}$  for Infaunal Bivalves, however their group also included the very small species which I excluded from this model. Thus, this number is likely to be somewhat high. For comparison, Brey's methods (2001, 2012) were used to estimate the energy per individual and estimate  $P/B$  based on energy and life history characteristics (Table A5). Allometric data was only available for the genus *Veneridae* (Butter clams), and yielded a  **$P/B = 0.410 \text{ yr}^{-1}$** . This value was used in the model, recognising that it could perhaps be somewhat low.

*Consumption:* As with MU, 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  $P/B$  (Harvey et al. 2010).

#### *Lingcod (LC)*

Adult lingcod (*Ophiodon elongatus*) 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 ( **$B = 0.33 \text{ g m}^{-2} \text{ yr}^{-1}$** ) of the values from three BC models (Ainsworth et al. 2002, Martell 2002, Preikshot 2007) was used as an estimate of density. This is implicitly for otter-absent areas as the models were derived for otter-absent systems.

*Production:* Recent work on LC populations for three offshore lingcod areas in BC (Cuif et al. 2009) led to an average  $r$  of 0.252. However, given that LC continue to be exploited by recreational fisheries, this was reflected in the  **$P/B = 0.50 \text{ yr}^{-1}$**  used, which is in the range between unexploited and exploited values discussed by Harvey et al. (2010).

*Consumption:* The average ( **$Q/B = 3.55 \text{ yr}^{-1}$** ) of the values from the Martell, Preikshot, and Ainsworth models was used.

*Diet:* First, because of their extensive foraging in deeper habitats not included in the study area, it was assumed that LC import 50% of their diet. The other 50% was divided into proportions similar to those published elsewhere (Beaudreau and Essington 2007, Tinus 2012): ODRF (0.15), PRF (0.05), FF (0.01), KC (0.1), and SG, MG, and SI with (0.06) each, and LC (0.01) (Table A3).

### *Other demersal reef fish (ODRF)*

The NEP has the world's greatest diversity of rockfish (*Sebastes* spp.) with over 65 different species (Hyde and Vetter 2007). These species are generally associated with rock reefs. While demersal fish species tend to get larger in deeper waters, where most of these spend their adult lives, the nearshore is home to most, earlier in their life history, 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 LC. Of the remaining species, the most dominant in this group are greenlings and black rockfish. The group also includes sculpins and other larger rockfish species such as cabezon and red Irish lord.

The average values from the "Other large rockfish" groups defined by Preikshot (2007) and Ainsworth (2002) gave  $P/B = 0.14$  and  $Q/B = 3.0$ . However, since these values yield a low  $P/Q$  ratio, a  $P/B = 0.24 \text{ yr}^{-1}$  (from Harvey et al. 2010) was used, and  $Q/B = 1.2 \text{ yr}^{-1}$  calculated using an assumed  $P/Q = 0.2$ . Ecopath was allowed to estimate **B** using  $EE = 0.8$ , the same value used by Harvey et al. (2010) for their Demersal Fish group. This is the only species for which these parameters were extensively revised during balancing (see below).

*Diet:* The diet of rockfish differs somewhat by species but 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 (Pauly and Froese 1996) are: finfish 13-90%; zoobenthos 5-70%; and zooplankton 3-20%. To ensure the diet was broadly based, it was structured to include: SI (0.25), equal parts MG and LZ (0.2), KC (0.1), equal parts (0.05) PRF and SG, some FF (0.02), and a possibility (0.01) of PI, LG, and SH, with a notable (0.1) cannibalism component.

### *Pelagic reef fish (PRF)*

This group includes species such as surf perch, tubesnouts, and pipefish that spend the majority of their life history in the water column, associated with either the kelp forests on rocky substrates. Surf perch were explicitly represented by Espinosa-Romero et al. (2011b), while

Harvey et al. (2010) defined a somewhat broader group termed Demersal Fish, that combined these pelagic species with the demersal ones.

A  $P/B = 2.0 \text{ yr}^{-1}$  and  $Q/B = 10.0 \text{ yr}^{-1}$  were used for this group. These values are slightly higher than those used by Harvey et al. (2010) to account for the shorter-lived characteristics of the group, while maintaining a P/Q value of 0.20, a standard value for fish (Harvey et al. 2010). As with the ODRF, Ecopath was used to estimate **B** with **EE = 0.8**.

*Diet:* Based on the data reported for a number of northeast Pacific species in FishBase (Pauly and Froese 1996), the prey of this group includes small forage fish, and both planktonic and benthic crustaceans. These are represented in the model as LZ and MG groups. The diet was therefore defined as largely LZ (0.42), MG (0.20), and KC (0.1), with equal (0.05) contributions from PI, LG, SG, SI and SH, and the possibility of early life history ODRF, PRF, and FF (0.01 each). The group forms a significant component of the diet of the larger fish groups.

#### *Forage fish (FF)*

This group is envisioned to include the small, seasonally abundant, schooling species. They are differentiated from PRF because of their seasonal aggregations that are important to many macro-organisms. In BC, this group includes, primarily herring (*Clupea pallasii pallasii*), sand lance (*Ammodytes hexapterus*), and sardines. All species were included as a single functional group since their ecological role is similar, as are their diets (see Pauly and Froese 1996). The composition of this group differs from that typically defined by other (more offshore fisheries focused) models of the area which include more oceanic species such as smelt and mackerel, and even juvenile walleye pollock, often treating herring separately.

Assuming this group is dominated by herring, the average  $Q/B = 4.75 \text{ yr}^{-1}$  from the Ainsworth, Martell, and Preikshot models was used. While the Q/B corresponded well to Harvey et al.'s (2010) forage fish group, the P/B average of 0.67 seemed low. A  $P/B = 1.5 \text{ yr}^{-1}$  based on an integrated forage fish value (Field 2004 cited in Harvey et al. 2010) was therefore chosen. Ecopath was allowed to estimate **B** based on an **EE=0.90** given the role of FF in the ecosystem.

*Diet:* Examining the diet from earlier models shows that juveniles 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 this translates into primarily LZ (0.75) and MG (0.14), some small portion of KC (0.03) and SG (0.05), and a possibility of LG, SG and SI (0.01).

#### *Kelp crab (KC)*

While serving a similar ecological role as small grazers, these animals contribute to the SO diet, thus warranting their own group. The group is typically dominated by Kelp Crab (*Pugettia producta*) but also includes decorator crabs and other small kelp-associated species.

*Biomass:* Ecopath was allowed to estimate **B** for this group based on a presumed **EE = 0.90**.

*Production:* Ainsworth et al.'s (2002) value of **P/B = 3.5 yr<sup>-1</sup>** was used for this group, which corresponded well with the value (3.41) estimated by Harvey et al. (2010) for small crustaceans.

*Consumption:* Ainsworth et al. (2002) estimated Q/B for this group at 14.0, while Harvey et al. (2010) used Q/B = 25 for small crustaceans. A **Q/B = 20.0 yr<sup>-1</sup>** was chosen.

*Diet:* Kelp crab are more herbivorous than their larger counterparts (Slater Museum 2014) so they were assigned a significant kelp component including OM (0.19) and Macro (0.1), with only a small (0.01) portion of Nereo because of its more exposed nature. Other significant components included MU and SI (0.2 each), and D and KD (0.1 each). The remaining 0.1 was assigned to SG (0.06), while allowing for predation (0.01 each) on SU, PI, LG, and MG.

#### *Other benthic invertebrates*

The sheer diversity of smaller marine benthic invertebrates makes creating such functional groups a significant challenge in any ecosystem model. The first step was to exclude small, infaunal invertebrates (e.g., polychetes, small bivalves, and the 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 considered to be primarily oceanic, and so were also excluded. The remaining species were divided into *Predatory invertebrates (PI)*, *Epibenthic*

*Large grazers (LG), Small grazers (SG), Meso-grazers (MG), and Sessile invertebrates (SI).* These groups are intended to comprehensively cover the nearshore invertebrate groups that occur on rock reefs, and allow representation of size-based trophic associations.

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

*Biomass:* All Bs were based on the BCCES data - dive surveys of rocky reefs in the study area (Martone et al., in prep. Table 4.3). Scaling applied the 10% kelp habitat assumption, with an additional 10% habitat suitability assumption. For P/B and Q/B, the available information for each group was considered separately.

#### *Predatory invertebrates (PI)*

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

*Production:* Harvey et al. (2010) estimated P/B = 0.52 for sea stars and 1.01 for predatory gastropods. Here the mean of these two values was chosen giving **P/B = 0.76 yr<sup>-1</sup>**.

*Consumption:* Harvey et al. (2010) estimated Q/B = 2.6 for sea stars and 6.73 for predatory gastropods. A value of **Q/B = 4.0 yr<sup>-1</sup>**, slightly lower than the mean because sea stars dominate the relative abundance in this group, was chosen.

*Diet:* PI feed principally on a diverse diet of other benthic invertebrates. Pisaster's feed primarily on MU, barnacles (SI), and limpets and snails (SG) while moon snails feed primarily on clams (OEC) (Harbo 1999). Since it is likely that other benthic invertebrates are also consumed by this group, a broad diet was assigned, with equal (0.2) proportions to MU, OEC, SG, and SI, 0.10 to D, and the remainder divided equally (0.02) among SU, KC, PI, LG, and MG.

This group is preyed upon by SO, LCC, LC, ORDF, and PI.

### *Large grazers (LG)*

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

*Production:* Harvey et al. (2010) estimated  $P/B = 0.753$  for an "Other Grazers" group that includes chitins and small gastropods. Lessard et al. (2007) estimated abalone mortality in the absence of sea otters at approximately 0.25. Given that this group is intended to represent all these species, the larger snails and chitins,  $P/B = 0.50 \text{ yr}^{-1}$  was used, the mean of these two values.

*Consumption:* Harvey et al. (2010) estimated  $Q/B = 8.9$  for the Other Grazer group, and 11.3 for the Large Cucumber group. The mean of these two values was chosen, giving  $Q/B = 10.1 \text{ yr}^{-1}$ .

*Diet:* This group is intended to include herbivores and thus diet is defined to be largely *Kelp Detritus* (0.68) and the *Other Macroalgae* (0.20) groups. The inclusion of large cucumbers in this group adds a significant *Detritus* (0.10) portion to the diet. The possibility of active grazing on either canopy kelp was allowed (0.01).

### *Small grazers (SG)*

This group includes active grazers too small to serve as sea otter prey (i.e., small snails and shrimp, limpets, periwinkles, small chitins). Since this group falls functionally between the large and meso grazers, values intermediate between these groups were used:  $P/B = 3 \text{ yr}^{-1}$  and  $Q/B = 14 \text{ yr}^{-1}$ .

*Diet:* Feeding primarily on large pieces of KD (0.83), this group is responsible for breaking down larger pieces of algae into smaller ones. A portion (0.15) of the diet was assigned to OM 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.

### *Meso grazers (MG)*

This group is comprised of grazing benthic invertebrates too small to be SO 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 Harvey et al. (2010), 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 range as high as 6.0. These values correspond well to the  $P/B = 3.41 \text{ yr}^{-1}$  used by Harvey et al. (2010) and that value is adopted that value here.

*Consumption:* Harvey et al. (2010) derived  $Q/B = 25$  from earlier models. However, this value led to respiration values that seemed excessively high. A lower  $Q/B = 15 \text{ yr}^{-1}$  was used to allow a lower respiration value.

*Diet:* Amphipods are mainly detritivores, while mysids eat primarily algae and detritus in addition to some infaunal benthic invertebrates and zooplankton (Wikipedia 2015a, b). However, the small crabs in this group are more predatory, potentially taking MU and OEC, as well as young stages of PI, and other MG groups. Since the grazers in this group continue the decomposition of detritus and algae into smaller particles (i.e., POM) suitable for filter feeders, D was assigned 0.5 of the diet, with equal proportions (0.10) to PP KD, OM, and cannibalism. The remaining 0.10 was divided between SH (0.08) and MU and OEC (0.01 each). This group can dominate the diet of larger animal groups such as PI, juvenile PRF, FF, and ODRF.

### *Sessile inverts (SI)*

This group of includes filter feeders (i.e., barnacles, tube worms, sponges, anemones, little cucumbers) that are too small to serve as SO prey. This diverse group is comprised of species from the Suspension Feeders, Deposit Feeders, Tunicates, and Barnacles groups defined by Harvey et al. (2010).

*Production:* Considering what might be the relative abundances of these groups in the study area, an arbitrary  $P/B = 2 \text{ yr}^{-1}$  was chosen. This is in the range of all the similar groups used by Harvey et al. (2010).

*Consumption:* Considering the relative abundances of these groups in the study area, an arbitrary  $Q/B = 13 \text{ yr}^{-1}$  was chosen. This is in the range of all the similar groups used by Harvey et al. (2010).

*Diet:* As filter feeders, this group will consume anything of an appropriate size including both zooplankton and phytoplankton. A balanced, diverse diet was therefore assigned including LZ (0.30), SH (0.30), PP (0.1), KD (0.15), and D (0.15).

#### *Large zooplankton (LZ)*

This group is comprised primarily of copepods, euphausiids, ichthyoplankton, and invertebrate larvae. Estimates of  $B = 16.3 \text{ g m}^{-2} \text{ yr}^{-1}$ ,  $P/B = 15.8 \text{ yr}^{-1}$ , and  $Q/B = 45.6 \text{ yr}^{-1}$  were based on the average used by Espinosa-Romero et al., Martell, Preikshot, and Ainsworth for similar groups. As with the other model-based biomass estimates, it was assumed these were for the otter-absent system as that corresponds to the time the models were developed.

*Diet:* A somewhat arbitrary diet was defined, dominated by PP (0.60), with contributions from SH (0.25), KD (0.10), and cannibalism (0.05).

#### *Small heterotrophs (SH)*

This group includes all heterotrophic organisms less than 200  $\mu\text{m}$  in size. Estimates of  $B = 11.7 \text{ g m}^{-2} \text{ yr}^{-1}$ ,  $P/B = 125 \text{ yr}^{-1}$ , and  $Q/B = 290 \text{ yr}^{-1}$  were based on the herbivorous zooplankton groups defined by Martell and Preikshot. A diet dominated by PP (0.8), supplemented by KD (0.10), with equal (0.05) parts D and cannibalism was defined. Production and consumption estimates correspond well with those used by Harvey et al. (2010) 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 West Coast is more

productive than Puget Sound. As with the other model-based biomass estimates, it was assumed to be for the otter-absent system, corresponding to the time of model development.

### *Phytoplankton (PP)*

Also called primary production, this group includes planktonic organisms that synthesise organic compounds from CO<sub>2</sub> and nutrients typically 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 (Barber 2007).

This model, and Ecopath models in general, appear insensitive to PP B and P/B values since PP is rarely modelled as a limiting resource. This model simply used the average from the other 4 models of the region (**B = 25 g m<sup>-2</sup> yr<sup>-1</sup>, P/B = 125 yr<sup>-1</sup>**).

### *Macroalgae*

Because of the putative role of canopy (or overstory) kelps as nursery habitat, and the apparently different roles played by the dominant species (Springer et al. 2007), the canopy kelp were separated into the annual kelp *Nereocystis macrofoliata* (Nereo), and the perennial kelp *Macrocystis pyrifera* (Macro). All other kelps were grouped into *Other Macroalgae* (OM), recognising that this is a large, diverse group.

### *Kelp production (P/B)*

Harvey et al. (2010) provided a detailed review of Nereo B and P/B, and concluded that the growth of individual sporophytes for rapidly growing annual species is better reflected in the P/B ratio, and not the B. The proposed **P/B = 43 yr<sup>-1</sup>** for Nereo was therefore accepted. As a perennial, Macro while potentially faster growing than Nereo at its peak growth rate, turns over less B in a season. In their study of Macro turnover in California, Reed et al. (2009) provide estimates of both standing stock and production from we estimated a **P/B = 6.08 yr<sup>-1</sup>**. The

diverse OM group includes all other species of fleshy macroalgae, including corallines. Harvey et al. (2010) assigned  $P/B = 15 \text{ yr}^{-1}$  to a similar group in Puget Sound and this value was adopted here.

### *Kelp Biomass (B)*

Kelp B was difficult to estimate for the entire study area not only because localised field studies tend to be at the scale of an individual kelp forest, but also because of high temporal (inter-annual) and spatial (across site) variability. Habitat suitability models have been used to estimate presence/absence of kelp over large areas (e.g., Gorman et al. 2013), and some studies have assumed general biogeographic distributions (e.g., Wilmers et al. 2012). 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 realised habitat were assessed for their suitability for scaling the kelp B.

The BCCES study collected B for Macro, Nereo, and a representative sample of understory kelp in otter-present and otter-absent study sites (Martone, unpublished). These values were compared to similar data but collected as the number of stipes (Watson and Estes 2011). Both data sets provide evidence of dramatic change in the abundance of kelp in response to grazing pressure, though the differences in relative change between the two studies is notable.

The scaling challenge is manifest at two scales. First, observed differences in B relate to kelp forest biomasses, and thus will provide information on the relative size of kelp forests in otter-present and otter-absent regions. But these data provide no information on the regional distribution and abundance of these kelp forests. Scaling kelp forest B to a regional study area thus requires an estimate of both change in local, kelp forest B, and change in regional distribution. The scaling must strive to estimate the amount of habitat realised by kelp in the study area.

Given the variability in sampling and the significant scaling challenges, Ecopath was allowed to estimate the B value based on the understanding that the otter-absent system is dominated grazers, a situation that leads to low kelp B values. Kelp groups should therefore have a high Ecosystem Efficiency (EE - represents the portion of a group's B accounted for in the model). A higher EE also agrees with the earlier assumption that SU in an otter-absent state are food limited. Assumed EEs of 10%, 90%, and 80% for Nereo, Macro, and OM respectively were assumed. These values consider the fact that Nereo is distributed in higher exposure areas where it is both more susceptible to export and less accessible to SU predation. While for OM, a lower value is reasonable as some species in this diverse group may be less predated by SU.

#### *Kelp Detritus (KD) and Detritus (D)*

Biomasses for the detritus groups are used only for plotting relative changes to the group. The actual **B** value is based on the flows from the other groups. Both Kelp Detritus (KD) and the main Detritus pool were set to an arbitrary value of 10.0. All groups were directed to Detritus except the 3 kelp groups, which were sent to the KD pool. The KD pool was then directed to the main D 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 (SU, LG, SG, MG, LZ, and SH) 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.

#### ***Fisheries***

Catch data for 5 commercial species were obtained from DFO for the 4 management areas within the WCVI study area for the years 1996 to 2008. The mean annual catch was used to balance the Ecopath model, but the catch was first scaled to the study area using habitat assumptions.

Scaling to habitat was done somewhat differently for each species. RSU were scaled using the 30% rocky reef habitat assumption; LCC, GC, and EC were scaled using the 30% soft bottom

assumption, and OEC were further restricted to shallower depths. Finally, the fisheries data showed that only about 10% of the LC were caught in the study area, thus LC landings were reduced from 0.407 to 0.0407. The observed and scaled catch is shown in Table A7.

### ***Model balancing***

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.

The derived values Respiration (**R**), and food conversion efficiency (**P/Q**) provide a simple diagnostic for evaluating the 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 (Christensen et al. 2008).

**P/Q** values were low (< 0.1) for SU, GC, and LG. Corresponding **R** values were quite high for SU and LG, but appropriately low for GC (even though it is twice as high as OEC, this could be explained by the energy required for nutrient pumping by deeply buried species). Thus, no adjustments were made to the GC parameters. Adjusting **Q/B** and **P/B** for SU was considered, however the parameters were reliably derived, and significant, perhaps unrealistic changes were required to bring the R and P/Q values within the recommended ranges. Given that the ranges are largely intended for fish species, and that SO 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.

However, **R** for ODRF (0.72) seemed low, though **P/Q** was acceptably in the middle of the fish range. Some juggling was necessary here because this group is widely trophically connected. Ultimately, both **P/Q** (0.24 -> 0.3 yr<sup>-1</sup>) and **Q/B** (1.2 -> 2.0 yr<sup>-1</sup>) were raised, giving a more reasonable (though not ideal) **R** = 1.3. This also brought the base parameters more in line with LC. However, this gave too much B and unbalanced the model, requiring an **EE** = **0.9** to balance the model.

## ***Model dynamics***

Having thus balanced the steady state, mass-balance model, the next task was reproducing the simulation of the trophic cascade currently underway on the WCVI. First, the dynamic control parameters were adjusted according to the guidance in Christensen et al. (2008). The parameters of interest here (on the Ecosim Group Info form) include Maximum relative feeding time (MRFT), Feeding Time adjustment Rate (FTAR), Handling time (HT), and Switching Power (SP).

MRFT was left at the default value of 2.0 for all groups except SO, which we allowed to increase their feeding time as necessary in the face of a changing diet by setting MRFT to 25.0.

Christensen et al. (2008) recommend changing the default FTAR value from 0.5 to 0 for all species except marine mammals. That advice was followed here.

The default HT (1000) assumes prey will be sufficiently rare in the system that handling times will not be relevant (Christensen et al. 2008). However, in systems as tightly coupled as the one considered here, it is reasonable to assume handling time would be important, and so HT was set to 3 for all species (the middle of the range suggested by Christensen et al. 2008).

Based on the understanding of SOs as an opportunistic and voracious forager, it is assumed they switch between prey opportunistically at a faster rate than determined simply by relative changes in prey abundance. The SP for SO was therefore initially raised from the default of 0 to 1.0, the value with the least dramatic effect on how fast a predator can switch between prey species (Christensen et al. 2008).

Vulnerability (**V**), the key dynamic parameter representing the strength of top-down control between each predator and its prey, was considered next. The parameterisation of V bears some consideration particularly where there is strong top-down control. For simplicity, only the top-down effects of SO on their prey groups was considered since a lowering of grazer realised habitat (and hence carrying capacity) is a pre-requisite of the observed trophic cascade.

Given the diversity of SO prey species, four groups were defined according to their accessibility and nutritional value to SO, and each group was assumed to have a different V to SO predation

(Table A8). Examination of hundreds of model configurations determined that without these within-SO differences in  $V$ , it is difficult for SO to suppress SU in the current model.

Understanding  $V$  is best done using Ecosim's time series fitting routine. This routine searches for  $V$ s for any selected predator-prey pairs to minimise the sum of squares between  $B$  predicted by the model and the  $B$  of a user-specified time series. We used a set of 9 time series based primarily on the BCCES data. These data informed the pre-otter and post-otter biomasses of the 8 invertebrate groups. Using space-for time substitution (Table A3), 3-point time series (1970, 2050, and 2100) were created to explore how the  $V$ s for the 4 SO prey groups varied in response to different parameterisations. The last time series represented sea otter population growth curve using the two-part logistic growth proposed by Nichol et al. (2009) and  $K$  of 8,303 predicted for an area of 1,304 km<sup>2</sup> (Gregr et al. 2008).

### ***Ecological realism***

The initial, scaled and balanced model had difficulty reproducing the trophic cascade while adhering to the presumed SO population growth curve. Forcing SO to adhere to its population growth curve led to limited top-down effects. This strongly suggests that if the  $B$  of SO prey is too abundant, a trophic cascade is unlikely. Since the SO carrying capacity was assumed to be accurate, further reduction in the  $B$  of SO prey were needed to simulate the trophic cascade.

SU population dynamics and the role of SU  $P/B$  in the simulation was considered, since a reduction in either this or  $B$  would reduce the prey available to SO over time, making it easier for SO to suppress the population. Evidence suggests that at high densities (as on urchin barrens) SU are often food limited, leading to significantly lower reproductive rates (Konar and Estes 2003). This implies the  $P/B$  ratio used in the balanced, grazer-dominant model is likely too high. SU  $P/B$  also exhibits high inter-annual variability and is sensitive to a range of oceanographic conditions (Carefoot 2010), including the presence/absence of kelp forests (Konar and Estes 2003). Clearly, a mean  $P/B$  for SU is somewhat simplistic. Nevertheless, since  $P/B$  is cannot be modified directly as part of an Ecosim simulation, it was assumed this variability would lead to a lower overall SU abundance over time, and so the effect was represented by reducing SU  $B$  further to a final  **$B = 29.0$**  g m<sup>-2</sup> yr<sup>-1</sup>.

Finally, the SO B in the balanced model was higher than predicted by the population model. Rather than further reduce the available prey base (and potentially unbalance the model) the **Q/B** ratio was simply increased from 102.2 yr<sup>-1</sup> to 120.0 yr<sup>-1</sup>.

### ***Mediation***

Kelp is believed to influence nearshore ecosystems through the provision of complex habitat, the attenuation of water movement, as well as enhanced secondary production (Duggins et al. 1989), the ecological benefits (i.e., supporting ecosystems services) are likely both diffuse and significant. Markel (2011) concluded that the available evidence supports the theory that increased primary production from kelp forests increases the abundance, biomass and diversity of lower trophic level invertebrates, and that this in turn supports a more abundant and diverse assemblage of primary and secondary predators. The effect extends to fishes, with those having multiple kelp-associated life stages (like nursery and foraging habitat for *Sebastes* species) showing the greatest response (Markel 2011).

It can thus be assumed that kelp increases the production of finfish through three mechanisms, increased recruitment, increased juvenile survival, and concentration of planktonic prey. These effects, while difficult to measure empirically, can nevertheless be represented in Ecosim. EwE implements mediation by changing the interaction between groups, modifying one group's search rate, Vulnerability, or Arena Area in response to the B of another. Mediation cannot be applied directly to the P/B of a particular group.

For simplicity (and lack of any quantitative information) the mediation effect was limited to the third of these mechanisms. The concentration of prey by kelp was represented by reducing the effective search area of finfish in response to increasing kelp B. A hyperbolic curve was used, as this is thought to be the most conservative (Harvey and Rose 2014), and parameterised using the most gradual setting (i.e., y intercept = 1.0). We applied the same functional form to all finfish-prey relationships in the model.

### ***Final parameterisation***

The Ecosim dynamics (FTAR, SP, and Vs) were tuned manually to the 9 time series described above. Extensive exploration of various FTAR, SP, and V values identified large regions of the parameters space where predator-prey oscillations of various periods, frequencies, and shapes manifest. Final parameter values for SO (**MRFT = 25.0, FTAR = 0.75, SP = 0.3**) were based on trends observed in the parameter exploration. The V scores (Table A8) were rounded to single precision, and levelled manually to maximise fit to the time series.

### ***Model performance***

Model fit was based largely on the sum of squares (SS) value from the time series fitting. This provided insight primarily into the magnitude and relative size of the vulnerabilities. The relative setting for FTAR, HT, and SP were determined experimentally. Throughout the process, consideration was also given to how well the model predictions corresponded with the observed diet of SO in otter-occupied areas, and the relative increase in kelp production. The stability of the population dynamics was also a factor.

*Fits to time series:* Estimation of the SS was dominated by the hypothesised SO population curve because it is empirically based, and because it provides a reasonable upper limit to the model B. The fit to the remaining 8 hypothesised B trends varied according the different parameters used. General observations over many parameter settings confirm that the trends of SU, PI, LG, GC, SG, and MU can be followed, but SI and MG often (and in the final model) trend in the wrong direction. This reluctance of the model to allow predictions of all groups to trend in the observed direction may be a problem with the trophic dynamics as defined, or perhaps important groups or interactions are missing.

*Correspondence to diet:* The observed diet of SO in areas of extended occupation was reported by Laidre and Jameson (2006) as MU and OEBC sharing about half the diet, with roughly equal parts LG and SI (0.15) and PI (0.1), with a contribution from LCC (0.05) and KC (0.05). The final predicted SO diet exhibited this diversity, but varied considerably in response to the initial diet, the vulnerabilities, and the FTAR and SP settings.

*Kelp production:* The recovery of kelp was allowed to emerge from the model rather than including available observations in the time series fitting. The predicted increase in kelp B helped to rank the different model dynamic parameterisations, as maximising kelp production was an explicit objective.

### ***Ecosim technical findings***

There are certain parameterisations under which the model will create a trophic cascade and a substantially smaller subset where this cascade does not create classic Lotka-Volterra predator-prey cycles. These cycles seemed most common with either low or high SP values (i.e., values outside the range 0.8 to 1.2 generally had some form of cycle).

The problem is most pronounced when trying to force certain behaviour (by modifying vulnerabilities) when sea otter prey biomasses are high (i.e., low EEs). The cascade also requires high EE values for kelp (a theoretical assumption borne out in the parameterisation).

The dynamic parameters Vulnerability and FTAR make the cascade possible. Vulnerability allows suppression of the prey populations, and FTAR allows the SO population to grow fast enough to initiate the cascade — without it, there is just an even lowering of the SO prey base. Group vulnerabilities were necessary to maximise fits to time series.

Fitted Ecosim models all exhibit an initial overshoot in the SO population. This overshoot is most likely a mathematical artefact related to how the Type 2 functional response is calculated on the steep part of the predator-prey curve, encountered when prey (e.g., SU, LG) are reduced to very low levels. The magnitude of this overshoot is influenced by the interaction between FTAR and SP. Increasing SO SP reduces the population required to initiate the cascade, and reduces the magnitude of the overshoot.

### ***Ecosystem services calculation and uncertainty representation***

The uncertainty in the Ecopath prediction of ecosystem service provision is based on a Monte Carlo simulation of Ecopath's base and diet parameters. The base parameters of the balanced model were permuted using a normal distribution centred on the value used in the balanced model, with a standard deviation proportional to the presumed accuracy (low, medium or high)

of the base parameter (Table A9). Diet parameters were all permuted using low accuracy, to allow the maximum range of potential models to be explored.

Permuted versions of otter-absent Ecopath models were repeatedly generated until a sample of 1000 balanced models was obtained. It was difficult to tell, *a priori*, how effectively the permutations would be at generating balanced models given the assigned standard deviations (i.e., it is reasonable to expect that excessive randomisation of the base and diet parameters would have a very low probability of generating a balanced model). A conditional reduction in randomisation 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. After considerable experimentation, the randomisation was configured with maximum number of 100 attempts, and a constriction of 5% of the standard deviation. To ensure the later scenarios were not overly constrained, no additional constrictions were applied after the first 10 balanced scenarios were obtained.

Randomised, balanced models were run through Ecosim to generate a corresponding 1000 alternate future scenarios. The B values from these paired models represent the variability in the predicted ecosystem service provisioning, on which the service calculations are based. For each ecosystem service calculation, an additional uncertainty was added to represent other uncertain aspects of the calculation, as described below.

*Value of existing fisheries:* This service was comprised of 5 established commercial species (SU, LCC, GC, OEC, and LC) closely associated with the modelled ecosystem. The catch value for the years representing otter-absent (1970) and otter-present (2050) states was calculated by multiplying B distributions generated using Monte-Carlo simulation by catch rate and landed value.

Caught biomass was calculated within the model using a constant catch rate, set in the 1970 Ecopath model. Thus, catch is always proportional to B for all fished species. Landed value can be highly variable, changing in response to a range of local and global social and economic factors. To account for this variability, the landed values for both the 1970 (otter-absent) and

2050 (otter=present) periods were sampled from a distribution of landed values with a mean and standard deviation calculated from 10 years (2001-2010) of regional catch data. The final values were differenced to estimate the change in the value of the catch.

*Nutritional supplement:* The dollar value of this indirect ecosystem service was based on trophic transfer efficiencies (TTE) between the different trophic levels, and the dollar value of the presumed beneficiaries (i.e., commercial species).

Three supplement levels were defined. Trophic level 3 (TL3) included forage fish (ODRF, PRF, and FF), TL2 included primary consumers such as grazers and zooplankton (KC, PI, LG, SG, MG SI, LZ); and TL1 included the kelp groups (Macro, Nereo, Other). The nutritional supplement of each trophic level was calculated separately.

$$\begin{aligned}
 \text{Supplement \$ Value} = & \sum_{i=1}^{N_{TL3}} (NPP_i * TTE1 * \frac{\$}{\text{tonne}}) + \\
 & \sum_{i=1}^{N_{TL2}} (NPP_i * TTE1 * TTE1 * \frac{\$}{\text{tonne}}) + \\
 & \sum_{i=1}^{N_{TL1}} (NPP_i * TTE1 * TTE1 * TTE2 * \frac{\$}{\text{tonne}}) \quad \text{Equation A1}
 \end{aligned}$$

For each group (i) in each trophic level (TL3, TL2, TL1), the value of the surplus production available as a nutritional supplement outside the modelled system 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 in the modelled system, surplus  $NPP = B * \frac{P}{B} * (1 - EE)$ . This surplus was scaled to valued commercial species by estimating the TTE. Two TTEs were used. The first (*TTE1*) representing transfer between predators and prey, was randomly sampled from a normal distribution parameterised (mean = 0.1013, standard deviation = 0.0581) according to Pauly et al. (1995). The second (*TTE2*) recognises that the TTE from primary production to mesozooplankton is higher, was therefore sampled from a distribution with mean = 0.25 (Wade 2000 cited in Perry and Schweigert 2008). Both TTEs were truncated at zero. The nutritional supplement B was multiplied by a value (\$/tonne) drawn from a triangular distribution bounded

by a 20 year average annual landed value (2001 to 2010) of the least and most expensive commercial finfish (i.e., rockfish at 1.74 \$/kg and halibut at 8.53 \$/kg) (Province of British Columbia 2014), with a mode of 2.77 \$/kg – the weighted average of the adjusted 10 years of annual landed value of all commercial finfish (i.e., halibut, lingcod, rockfish, and salmon).

*Carbon sequestration:* Using just the three kelp species, change in B from an otter-absent to an otter present system was scaled to study area and converted to NPP of carbon. The annual dollar value was obtained by estimating the proportion of the carbon lost to deep flux, and multiplying it by the average price (Equation 2).

$$\text{Annual \$ Value} = \text{Kelps } B * \frac{P}{B} * \%D * \%C * \text{Deep Flux} * \frac{\text{mm } CO_2}{\text{mm } C} * \frac{\$}{\text{tonne } CO_2} \quad \text{Equation A2}$$

Annual value depends on net primary production (NPP = B \* P/B). B and P/B for the three kelp groups were combined by summing B and calculating a weighted average of the P/Bs. The resulting NPP, in wet tonnes/km<sup>2</sup>/year, was converted to total carbon using % Carbon (%C=26.6, SD=2.8) and % Dry (%D=17.3, SD=1.92) values taken from Wilmers et al. (2012), measured for giant kelp. It was assumed that %Dry = 1 - %Wet, the reported value.

The proportion transported to deep flux (i.e., how much of the biomass goes to the deep ocean) was estimated by randomising the surplus kelp-derived carbon into 3 phases, beach wrack, deep ocean flux, and the food web. This was done by first generating a random proportion lost to wrack, and then the proportion lost to deep flux. The remainder was used in the secondary production estimate (above). The wrack portion was sampled using a triangular distribution with the peak at 0.05, and the base extending from 0.01 to 0.1. The deep flux was then taken from the remainder using a proportion sampled using a triangular distribution with the peak at 0.3, and the base extending from 0.1 to 0.5.

The 2014 mean price (\$12/tCO<sub>2</sub>) was calculated from data provided by the California Carbon Exchange (CPI 2016). Finally, since B is in C and \$ is in CO<sub>2</sub>, a conversion factor for C equivalents was applied using the molecular mass (mm) ratio (CO<sub>2</sub>/C = 44 g/12 g), giving \$44/tC.

*Tourism:* Martone et al. (unpublished data) used choice experiments to estimate the value of sea otters to tourism on Vancouver Island, British Columbia. They estimate visitors to Vancouver Island would be willing to pay (WTP) between \$144-315 dollars more for a higher chance of seeing sea otters, and found that 27.6% of visitors were planned on engaging in wildlife tours. To estimate the value to tourism, this per visitor value was multiplied by potential number of visitors (obtained by combining survey data on destination with Parks Canada data on attendance).

A per visitor value was sampled from a uniform distribution using the observed range of WTP values. Number of visitors was drawn from a normal distribution using the average and standard deviation from 10 years of visitation data to Pacific Rim National Park, at the southern end of the study area (Parks Canada 2014). The uncertainty in the WTP from the choice experiment arguably integrates (implicitly) much of the uncertainty facing tourists.

*Table A1: Abbreviations used throughout the appendix.*

<b>Abbreviation</b>	<b>Description</b>
B	Density (in g m <sup>-2</sup> ), termed Biomass in the Ecopath model
P/B	Production/Biomass ratio - the net annual production of the species or group.
Q/B	Consumption/Biomass ratio - the net annual consumption by the species or group.
FTAR	Feeding Time Adjustment Rate: Determines how fast organisms adjust feeding times in effort to stabilise consumption rate.
V	Vulnerability: The strength of the effect a predator has the carrying capacity of its prey.
SP	Switching Power: The speed with which a predator can change its diet, beyond that determined by the prey biomass proportions.
EE	Ecotrophic Efficiency: The proportion of a group that is explicitly accounted for in the model.
HT	Handling Time: The time required by a predator to handle prey items.
SO	Sea otter
SU	Sea urchin
LCC	Large commercial crab (Dungeness and red rock)
GC	Geoduck clam
MU	Mussels
OEC	Other edible clams (e.g., butter, littleneck, manila, and cockles)
LC	Lingcod
ODRF	Other demersal reef fish (e.g., kelp greenlings, black rockfish)
PRF	Pelagic reef fish (e.g., surf perch)
FF	Forage fish (e.g., herring, sandlance)
KC	Kelp crab
PI	Predatory invertebrates (e.g., sea stars, welks, moon snails)
LG	Large grazers (e.g., turban snails, chitins, large cucumbers, and abalone)
SG	Small grazers (e.g., shrimp, periwinkles, limpets)
MG	Meso grazers (i.e., many small crustaceans)
SI	Sessile invertebrates (e.g., barnacles, sponges, anemones)
LZ	Large zooplankton (e.g., copepods, ichthyoplankton, invertebrate larvae)
SH	Small heterotrophs
PP	Primary production
Macro	Macrocystis (giant kelp)
Nereo	Nereocystis (bull kelp)
OM	Other macroalgae (i.e., midwater and bottom kelps)
KD	Kelp detritus
D	Detritus

Table A2: Production (P/B) and consumption (Q/B) rates; local, observed biomass (B, g m<sup>-2</sup>) and proportional change ( $\Delta B$ ) in otter-absent and otter-present systems; and B scaled to the study area for the two states. Shaded values were used to create the predicted time series used for Vulnerability fitting. Values in italics were input to the Ecopath model. See text for details about data sources.

Species/Group	P/B	Q/B	B (g m <sup>-2</sup> yr <sup>-1</sup> ) Observed		$\Delta B$	B (g m <sup>-2</sup> yr <sup>-1</sup> ) Scaled		Source
			Absent	Present		Absent	Present	
Sea Otter	<i>0.186</i>	<i>120</i>	89	8302	93.28	<i>0.000585</i>	<i>0.0468</i>	Gregr
Sea Urchin	<i>0.244</i>	<i>10.9</i>	290	25	0.0086	<i>29</i>	<i>0.250</i>	Watson
Large Commercial Crab	<i>1.5</i>	<i>4.25</i>	--	--	--	--	--	Estimated
Geoduck Clam	<i>0.048</i>	<i>2</i>	700	560	0.80	<i>70.0</i>	<i>56.0</i>	ADFG
Mussel	<i>0.428</i>	<i>1.42</i>	82600	57100	0.69	<i>82.6</i>	<i>57.1</i>	Singh
Other Edible Clam	<i>0.41</i>	<i>1.37</i>	6462	--	--	<i>19.39</i>	--	Derived
Lingcod	<i>0.5</i>	<i>3.55</i>	--	--	--	<i>0.33</i>	--	Earlier models
Other Demersal Reef Fish	<i>0.3</i>	<i>2</i>	--	--	--	--	--	EE estimated
Pelagic Reef Fish	<i>2</i>	<i>10</i>	--	--	--	--	--	EE estimated
Forage Fish	<i>1.5</i>	<i>4.75</i>	--	--	--	--	--	EE estimated
Kelp Crab	<i>3.5</i>	<i>20</i>	--	--	--	--	--	EE estimated
Predatory Invertebrates	<i>0.76</i>	<i>4</i>	60.0	50.6	0.84	<i>3.0</i>	<i>5.1</i>	BCCES
Large Grazers	<i>0.5</i>	<i>10.1</i>	142	1.66	0.01	<i>7.1</i>	<i>0.2</i>	BCCES
Small Grazers	<i>3</i>	<i>14</i>	19.5	65.8	3.37	<i>2.0</i>	<i>6.6</i>	BCCES
Meso Grazers	<i>3.41</i>	<i>15</i>	39.1	7.67	0.20	<i>1.95</i>	<i>0.8</i>	BCCES
Sessile Invertebrates	<i>2</i>	<i>13</i>	98.9	565	5.71	<i>4.94</i>	<i>56.5</i>	BCCES
Large Zooplankton	<i>15.8</i>	<i>45.6</i>	--	--	--	<i>16.3</i>	--	Earlier models
Small Heterotrophs	<i>125</i>	<i>290</i>	--	--	--	<i>11.7</i>	--	Earlier models
Phytoplankton	<i>125</i>	<i>0</i>	--	--	--	<i>28.0</i>	--	Earlier models
Bull Kelp	<i>43</i>	<i>0</i>	1405	985	0.701	<i>253</i>	<i>177</i>	BCCES
Giant Kelp	<i>6.08</i>	<i>0</i>	188	2932	15.6	<i>33.8</i>	<i>528</i>	BCCES
Understory Kelp	<i>5</i>	<i>0</i>	225	1246	5.53	<i>40.5</i>	<i>224</i>	BCCES

Table A3: Diet Matrix.

	Sea otter	Sea urchin	Large Commercial Crab	Geoduck	Mussels	Other edible clams	Lingcod	Other demersal reef fish	Pelagic reef fish	Forage fish	Kelp crab	Predatory inverts	Large grazers	Small grazers	Meso grazers	Sessile inverts	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
Large Commercial Crab	0.05	0	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Geoduck	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 crab	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 inverts	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 inverts	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	0.05	0.05	0.01	0	0	0	0	0.08	0.3	0.25	0.05
Primary production	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 A4: Energy estimates from mean wet weight and energy density estimates (Joules - Brey et al. 2012) for use in the P/B estimation tool.

Species/Group	mg WM	J/mg WM	J/individual
<i>Cancer magister</i>	750,000	3.988	2,991,000
<i>Panopea generosa</i>	1,000,000	3.929	3,929,000
Genus <i>Strongylocentrotus</i>	186,000	1.622	301,692
Family <i>Veneridae</i>	71,799	1.309	93,985
Genus <i>Mytilus</i>	45,650	3.2968	150,499

Table A5: Settings used to calculate P/B according to Brey (2012).

Taxon	Body Mass (J)	Z (m)	Mo	Cr	Ec	In	Se	Cr	He	Om	Su	P/B (yr <sup>-1</sup> )
<i>Cancer magister</i>	2991000	30	0	1	0	0	0	1	0	1	1	0.2781
<i>Panopea generosa</i>	3929000	10	1	0	0	1	1	0	1	0	1	0.1251
<i>Strongylocentrotus</i>	301692	10	0	0	1	0	0	1	1	0	1	0.2438
Family <i>Veneridae</i>	93985	0.1	1	0	0	1	1	0	1	0	0	0.4095
Genus <i>Mytilus</i>	150499	0.1	1	0	0	0	1	0	1	0	0	0.4281

Temperature set to 15C for all groups; All are marine and exploited.

Table A6: Allometric estimate of B for Other Edible Clams based on mean weight and density.

Species	Length (mm)	Alpha (x 10 <sup>-4</sup> )	Beta	Weight (g)	B (g) at 30/m <sup>2</sup>	B (g) at 130/m <sup>2</sup>	mean B (g m <sup>-2</sup> yr <sup>-1</sup> )
Butter	63	2.32	3.16	111.101	3333	14443	8888
Littleneck	38	2.73	3.04	17.373	521	2258	1390
Manila	68	2.77	3.00	86.922	2608	11300	6954

$W (g) = a * L (mm) ^b$  from Bradbury et al. 2005.

*Table A7: Reported mean annual (1983 - 2008) catch for the 5 commercial species in Fisheries and Oceans WCVI statistical areas (23 through 26), the standard deviation, the scaled 1970 landing rate (based on 3043 km<sup>2</sup>), and the resulting 2050 landing rate.*

<b>Species</b>	<b>Catch (tonnes)</b>	<b>Std. Dev.</b>	<b>1970 Landings (t km<sup>-2</sup> yr<sup>-1</sup>)</b>	<b>2050 Landings (t km<sup>-2</sup> yr<sup>-1</sup>)</b>
Clam	297	211	0.0976	0.0696
Crab	251	102	0.0825	0.0
Geoduck	806	563	0.265	0.214
Lingcod	1239	702	0.0407	0.124
Sea urchin	200	116	0.0657	1.16E-4

*Table A8: Classification of functional groups into vulnerability classes based on understanding of ecological role and interaction with sea otters.*

<b>Species/Group</b>	<b>Accessibility</b>	<b>Value</b>	<b>Vulnerability</b>
Urchin	High	High	
Large grazer	High	High	1000
Large commercial crab	High	High	
Mussels	High	Moderate	400
Geoduck	Low	High	200
Other edible clams	Moderate	Moderate	
Kelp crabs	Moderate	Low	
Predatory Inverts	High	Low	100
Sessile Inverts	High	Low	

Table A9: Estimated data quality for the main model parameters.

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	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 crab	Low	Low	Low
Predatory inverts	Low	Medium	Medium
Large grazers	Low	Medium	Medium
Small grazers	Low	Medium	Medium
Meso grazers	Low	Medium	Medium
Sessile inverts	Low	Medium	Medium
Large zooplankton	Low	Medium	Medium
Small heterotrophs	Low	Medium	Medium
Primary production	Low	High	--
Nereocystis	Low	High	--
Macrocystis	Low	High	--
Other macroalgae	Low	High	--